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THE UNIVERSITY OF ALBERTA

PATTERNS OF BEHAVIOUR AND PERFORMANCE OF WAPITI (*CERVUS ELAPHUS NELSONI*) IN THE BOREAL MIXED WOOD FOREST

by

© C. CORMACK GATES

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL PULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

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DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

FALL, 1980

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled PATTERNS OF BEHAVIOUR AND PERFORMANCE OF WAPITI (CERVUS ELAPHUS NELSONI) IN THE BOREAL MIXED WOOD FOREST submitted by C. CORMACK GATES in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in WILDLIFE PRODUCTIVITY AND MANAGEMENT.

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ABSTRACT

This study was conducted to investigate the behaviour and productivity of wapiti in relation to seasonal changes in physical and biotic elements of a boreal mixed wood environment of central Alberta. The study herd was composed of nine tame animals, including four calves and five yearlings beginning in 1977.

Foraging and resting dominated the activities of the wapiti throughout the year. Seasonal activity budgets were influenced to the greatest extent by forage factors. As forage quality and availability declined, the amount of time allocated to foraging increased. Strategic seasonal shifts in foraging frequency were viewed from the perspective of optimization of time allocation and energy balance. It was suggested that wapiti tended to minimize the amount of time spent foraging during seasons when high quality forage was abundant. There appeared to be an upper limit to the amount of time which could be used for foraging. When time was limiting, maximization of energy intake appeared to be the best strategy to pursue. Distances travelled while foraging were higher when forage quality and abundance were high. This reflected the intensity of searching for acceptable food items during periods of forage scarcity.

The temporal nature of the forage resource appeared to influence social behavior; wapiti tended to be less gregarious during periods of forage abundance. This was.

viewed both as an antipredator strategy and as a feeding strategy.

Frequency distribution of daily activities followed two basic patterns which differed among seasons. During fall and winter activity was polyphasic with alternating foraging and resting bouts occurring in approximately 4 or 5 cycles over a 24 hour period. During spring and summer the pattern was biphasic, with foraging peaks occurring around sunrise and sunset. Endogenous factors related to digestive functions and energy balance were discussed as determinants of the polyphasic pattern. Daily patterns in the thermal environment and insect annoyance were probably the most important factors determining the biphasic cycles.

Habitat selection was examined in relation to a number of biotic and physical factors. The response of wapiti differed for different activities. Phenological succession and snow conditions were the most influential factors determining the choice of foraging habitat. Wapiti tended to feed in habitats offering the earliest available green growth in the spring (sedge wetlands) and shifted from grazing in meadows to browsing in poplar forest then back to meadows as snow cover accumulated and receeded. Snow depths greater than 30 cm resulted in a major shift from grazing to browsing. Overall, wapiti exhibited a strong tendency to feed in meadows.

Selection of foraging habitat was affected only slightly by weather, while selection of resting sites was

strongly influenced by thermal conditions. Solar radiation exerted a maximum effect in late summer and fall when ambient temperature was high. Wind was an important factor determining shelter-seeking during January and February when ambient temperatures were low. The wapiti responded to insect annoyance by selecting a resting site which offered some relief.

The role of seasonal changes in insulation was discussed as a factor determining responses to the thermal environment. Responses varied seasonally depending on thermal insulation and the range of prevailing meteorological conditions. Snow cover and plant phenology were the major environmental influences determining selection of foraging habitat and food habits.

Seasonal weight dynamics of the wapiti were correlated with variations in certain environmental parameters. Diet quality, a function of forage availability and quality; appeared to be the dominant factor influencing weight change. The apparent duration of negative energy balance during the winter was 135 days. Weight gain began in the spring when green forage became abundant. Growth patterns differed among age/sex cohorts. The effects of age, body composition, reproductive status, and rutting activity were discussed. The effects of insect harassment on summer growth were assessed and the influence of disturbance on energy balance was discussed.

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Chapter 1

GENERAL INTRODUCTION

INTRODUCTION

Field ethology on large mammals was pioneered in Africa in the early 1950's (Leuthold 1977). Initially emphasis was placed on studies of social behaviour; however, in recent years field studies have stressed ecological aspects of behavior (Geist 1971b, Jarman 1974). Research has shifted from a phase of mainly descriptive work (Struhsaker 1967) towards functional interpretation of behavioural patterns (Geist 1979). The close relationship between ungulate ethology and ecology is now commonly acknowledged while in the past these disciplines unfortunately often were divided (Leuthold 1977).

Ungulates exhibit an array of morphological and physiological attributes which are often obviously adaptive to specialized life styles, physical environments, food habits, and antipredator tactics. Similarly, ungulate behaviour exhibits degrees of specialization. In general, behaviour shows heritable variation and natural selection will favour those individuals which contribute most effectively to subsequent generations. Consequently, the average behaviour of a population will tend to evolve in the direction of characteristics which are maximally fit for prevailing social and physical environments (Pyke *et al.* 1977).

The interaction between animal and environment is moderated by behaviour within the constraints of morphology or physiology. Behavioural responsiveness is seen in foraging patterns and diet selection (Jarman 1974, Ellis *et al.* 1976), habitat selection (Smith and Dawkins 1971), and in allocation of time to a number of possible activities (McFarland 1977). The ability of animals to cope with environmental contingencies is reflected in growth and reproductive success.

Although the behavioural and physiological performance of a species may show variation among environmental settings, much can be learned of its characteristics by detailed study in any natural environment. As patterns of behaviour are identified as recognizable characteristics of the species, responses in any natural environment become more predictable. Deviations from expected responses and normal behaviour patterns can be suspected as effects of extraneous disruptive influences such as human activity. It is important to gain insight into the nature of normal animal-environment interactions in order to assess the impact of disturbance factors. Detailed knowledge of behavioural performance of wild ungulates also is useful in designing intensive or enhanced management programmes. The proper balancing of habitat types requires information on foraging habits, escape responses, shelter-seeking behaviour, and social behaviour. Similarly, amelioration or avoidance of disruptive effects of industrial activity and

other potential human disturbances requires detailed knowledge of species characteristics.

The present study was conducted to investigate responses of the American elk or wapiti (*Cervus elaphus nelsoni*) to seasonal changes in physical and biotic elements of a study area located in the boreal mixed wood forest. Seasonal and daily patterns of behaviour and habitat selection were studied and animal performance was tracked using weight change as a reference.

Although Leuthold (1977) cautions against uncritical interpretion of results from studies of captive animals, the conditions of this research were close to ideal. The wapiti were tame, thereby permitting close observation, and were required without aid to perform as best they could in a seasonally stochastic, largely unaltered, natural environment. Their behaviour and performance were studied during a complete annual cycle. The use of tame animals was justified by the detailed information it was possible to collect. Other researchers in Alberta had previously experienced difficulty in maintaining continuous visual contact with wild free ranging wapiti without disturbing them.

STUDY ANIMALS

Wapiti used in this study were obtained as 2 - 24 hour old calves in 1976 from the Sybille Wildlife Research Station in Wyoming and in 1976 and 1977 from the University

of Alberta Research Station. All were hand-raised on milk replacers (Appendix 1). The yearlings were used previously for physiological studies (Gates and Hudson 1978, 1979). All of the elk were habituated to the presence of the author. The group was released in the study area at the beginning of September, 1977. Throughout the study they were free to forage and were not supplemented with food. Salt blocks were provided. One month was allowed for accommodation to their new environment prior to the start of data collection. Initially, the herd consisted of 2 yearling bulls, 3 yearling cows, 1 male and 3 female calves. The three cows gave birth to calves during the summer of 1978.

STUDY AREA

The study site was located in the Cooking Lake moraine of central Alberta. It was approximately 60 ha in size and was bounded by a 2-meter game fence. The topography was rolling hills and shallow basins, typical of dead ice moraine. The region is considered to be on the southern fringe of the boreal mixed-wood forest (Rowe 1972) with some components resembling aspen parkland.

The area is subject to a continental climate with long cold winters, short warm summers and wide diversions from average conditions. The mean length of the frost free period is 100 days and the average degree-days above 5.6°C is 2200 (Anonymous 1976). The average number of days with maximum temperature of 4.4°C or higher in January and February is

10. Mean annual snowfall is 127 cm and total annual precipitation averages 45.7 cm. There are only approximately 50 hours per year with winds equal to or exceeding 51 km/hr.

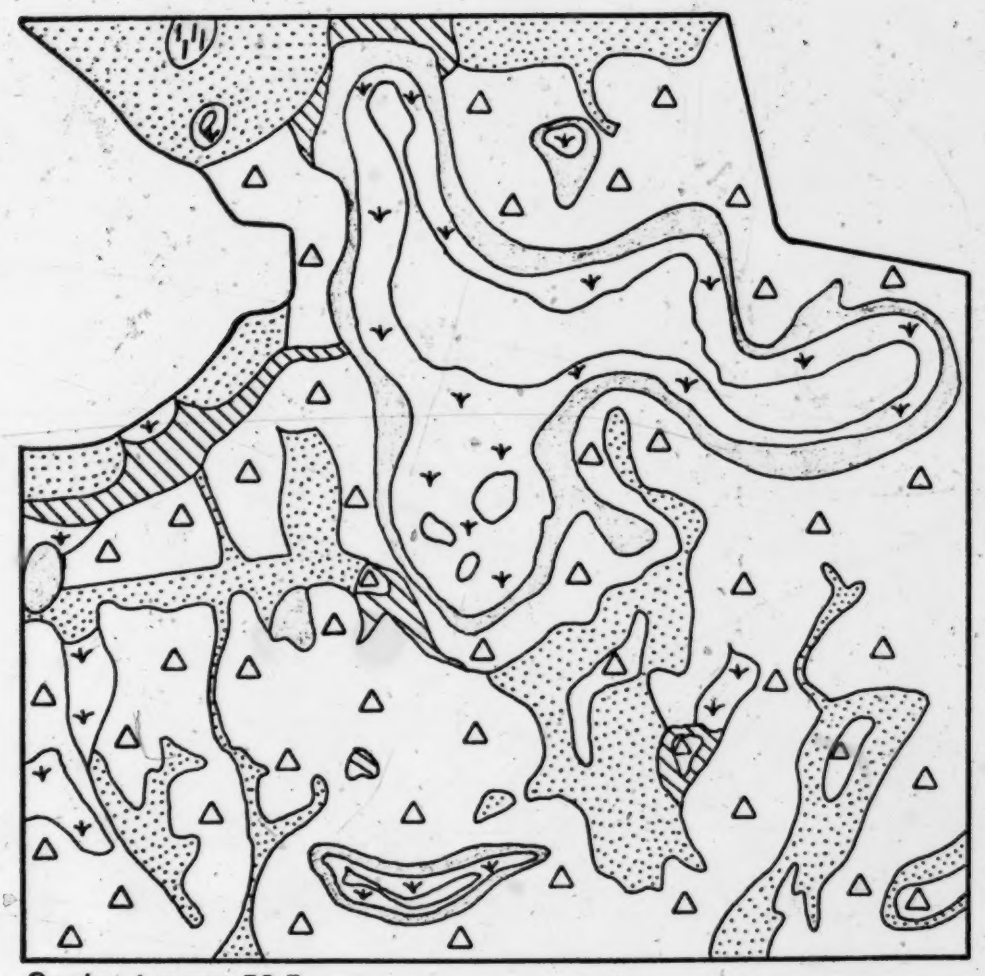
Habitat Types

The vegetative cover was characterized grossly into a number of types for the purpose of this study. A map of the vegetative cover types is displayed in Fig. 1. Poplar forest (*Populus* spp.) was the dominant type, occupying about 47% of the area. Depending on moisture conditions two species of poplar dominated the forest overstory; aspen poplar (*P. tremuloides*) in the drier locations and balsam poplar (*P. balsamifera*) in the moister sites. The understory was well-developed. It was composed of a number of shrub species including in order of importance: beaked hazelnut (*Corylus cornuta*), saskatoon (*Amelanchier alnifolia*), cherry (*Prunus pennsylvanica* and *P. virginiana*), raspberry (*Rubus melanolasius*), dogwood (*Cornus stolonifera*) and gooseberry (*Rubus hirtellum*).

Although white spruce (*Picea glauca*) is the dominant climax species in this forest zone, it was poorly represented in the study area and adjacent country. This is typical of poplar forests in the region which have been subject to frequent burning (Rowe 1972). Dendrochronological measurements of aspen suggested the area had been last burned about 40 years earlier.

Meadows were the next most important vegetation type covering 23.5% of the area. Local differences in drainage

Figure 1.1 Cover map of the study area.



Scale: 1 cm = 58.7 m

LEGEND

- Water
- Sedge wetland
- Willow fringe
- Lowland meadow
- Upland meadow
- Forest
- Posts

and soil moisture gave rise to three readily identifiable communities in the meadow cover type. The driest sites were occupied by a shrub-grass community in which brome (*Bromus pumpellianus*) was the dominant species and snowberry (*Symphoricarpos* spp.), saskatoon and rose (*Rosa* spp.) were the major shrubs in order of importance. There were relatively few sites where this community was present and since they were associated with upland meadows they were treated as part of that cover type.

Upland meadows developing under more mesic conditions occupied 19.1% of the study area. The two dominant plant species were brome and bluegrass (*Poa* spp.). Minor grasses were timothy (*Phleum* spp.) and wheatgrass (*Agropyron* spp.). In the lower lying meadow areas (lowland meadows) reedgrass (*Calamagrostis* spp.) was important in addition to brome and bluegrass. Lowland meadows occupied 4.4% of the area. In all meadow types forbs were seasonally important. The major species were dandelion (*Taraxacum officinale*), vetch (*Vicea americana*) and Canada thistle (*Circium arvense*). Poplar suckers were common at the edges of meadows adjacent to forest stands.

Wetlands were surrounded by willow fringes (*Salix* spp.) which occupied about 12% of the study area. In areas of shallow water or intermittently flooded sites, sedges dominated. The principal species was *Carex atheroides*. Around the edge of standing water there was usually a narrow fringe of bulrushes (*Scirpus* spp.). Sedge wetlands occupied

11.5% of the area.

One remaining physiographic feature which assumed unanticipated importance during the study was an area in upland meadow used for storing fencing supplies, creosote treated posts and rolls of wire. It occupied an insignificant area in the order of 100 square meters. The remainder of the study area was covered by shallow ponds.

Prior to being fenced, the study area was occupied by indigenous populations of moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*). Although the first two species were abundant, background utilization of the forage resource appeared to be light. During the study several moose and white-tailed deer frequented the enclosure.

Seasonal Changes in the Environment

Since maintenance behaviour is strongly influenced by the seasonal chronology of plant phenology, snow conditions and temperature, the following descriptions of environmental conditions provide a framework for interpreting observed patterns of behaviour and performance. Eight 'seasons' were subjectively delineated on the basis of changes in snow cover, plant phenology and temperature (Table 1.1).

The study began in fall, 1977 . Leaf abcission in the deciduous forest occurred at the beginning of this period. With successive frosts, senescence of forbs and curing of grasses progressed throughout the fall. Among the grass species, bluegrass retained the greatest amount of green

Table 1.1. Observation dates in each season.

Season	Observation Dates Year	Month	Day	Season	Observation Dates Year	Month	Day
Fall	1977	09	28	Spring	1978	05	03
		10	06			05	04
		10	17			05	09
		10	18			05	10
		10	24			05	11
		10	25			05	16
		11	05			05	17
		11	06			05	18
		11	08			05	21
		11	10			05	23
		11	12			05	25
		11	19			06	01
		11	21			06	02
						06	05
Early Winter		11	29			06	06
		11	30				
		12	17	Summer		06	21
		12	18			06	23
		12	19			06	30
		12	21			07	01
						07	03
Mid Winter	1978	01	04			07	04
		01	05			07	07
		01	06			07	12
		01	21			07	13
		01	22			07	14
		02	02			07	17
		02	03			07	18
						07	20
Late Winter		02	21			07	25
		02	22			07	26
		02	23			07	28
		03	07			07	29
		03	08				
				Late Summer		08	14
Early Spring		03	27			08	15
		03	28			08	16
		03	29			08	17
		04	25				

leaf . Brome grass, the other major species in meadows, cured comparatively early and had a greater amount of stem material than the beginning of November freezing temperatures began to persist during the daylight hours and ponds developed a cover of ice. The first permanent snow cover fell in mid November, although it was less than 5 cm deep. Mean weekly temperature declined from 9.0°C at the beginning of October to -9.0°C by the last week in November when the 'early winter' season started.

'Early winter' was characterized by colder temperatures than during the fall. Snow cover gradually increased in depth to about 20 cm by the third week in December. During the last few days of December and early January, successive heavy snow falls resulted in an accumulation of between 35 and 45 cm. Apart from woody plants, the only other forage protruding through the snow cover were the tall culms of brome grass and stems of common nettle (*Urtica gracilis*). Ambient temperatures during mid winter ranged widely (-30°C to +5°C) as periods of intense cold alternated with brief warm spells.

In late February, a chinook signalled the arrival of 'late winter'. Small patches of meadow were exposed from snow cover, particularly on knolls and south facing slopes. Warmer temperatures and increasing solar radiation resulted in the formation of a dense crust on the snow cover in the forest, and compaction and increased density in the meadows. Snow depth gradually decreased and meadows began to clear.

By late March, most of the meadow area was snow free and snow was disappearing rapidly in the forested areas.

The period between March 16 and April 30 was designated 'early spring'. The meadows were completely free of snow by the end of March and most of the snow cover in the forests had melted. By mid April, ambient temperatures were sufficiently high to result in the disappearance of ice in the wetland areas. The first evidence of a resurgence of plant growth occurred at that time in the wetlands where sedges began to sprout. Initiation of growth of grasses in the meadows was first noted on April 25, although the new growth did not achieve sufficient length to permit grazing until the first week in May. This signalled the arrival of spring.

'Spring' was a period of warmer temperatures and an abundance of new forage. Grasses in the meadows and forests grew rapidly during this time. Leaf development on woody plants began about May 8 with leaf flush occurring about May 17. By May 26 shrubs and trees had attained full foliage.

After the first week of June until the end of July, grasses entered the reproductive phase of their annual cycle. During the early part of this 'summer season', forbs achieved dominance. Ambient temperatures reached their maximum.

During 'Late summer' forbs began to decline in abundance and grasses began to cure. The consequence was an obvious decline in green leafy forage in the meadows.

A summary of meteorological conditions in the study area during observation periods is provided in Table 1.2.

Table 1.2. A summary of meteorological conditions recorded by the observer during observation periods in each season of the study.

Season	Variable	Mean	Standard Error	Minimum	Maximum
Fall	Solar Rad (W/m^2)+	21.8	1.13	0.0	87.2
	Wind (m/sec)	1.1	0.04	0.0	5.4
	Temperature (°C)	0.8	0.39	-30.0	17.0
Early Winter	Solar Rad (W/m^2)	5.4	0.70	0.0	48.8
	Wind (m/sec)	2.2	0.13	0.0	8.9
	Temperature (°C)	-6.1	0.52	-25.0	4.0
Mid Winter	Solar Rad (W/m^2)	13.1	1.22	0.0	59.3
	Wind (m/sec)	2.1	0.14	0.0	8.9
	Temperature (°C)	-13.4	0.50	-23.0	2.0
Late Winter	Solar Rad (W/m^2)	27.0	1.41	0.0	80.2
	Wind (m/sec)	4.0	0.23	0.0	13.4
	Temperature (°C)	2.1	0.24	-10.0	10.0

Early	Solar Rad (W/m²)	30.5	1.37	0.0	62.8
Spring	Wind (m/sec)	3.4	0.22	0.0	13.4
	Temperature (°C)	6.32	0.28	0.0	17.0
Spring	Solar Rad (W/m²)	25.2	0.96	0.0	76.7
	Wind (m/sec)	0.7	0.05	0.0	5.4
	Temperature (°C)	11.5	0.20	2.0	26.0
Summer	Solar Rad (W/m²)	44.0	0.87	0.0	76.7
	Wind (m/sec)	0.5	0.03	0.0	2.7
	Temperature (°C)	15.2	0.16	7.0	27.0
Late	Solar Rad (W/m²)	16.9	1.37	0.0	62.8
Summer	Wind (m/sec)	0.03	0.01	0.0	0.9
	Temperature (°C)	11.1	0.25	4.0	19.0

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*watts per square meter

Chapter 2

SEASONAL MAINTENANCE BEHAVIOUR

INTRODUCTION

McFarland (1977) hypothesized that animals deploy mutually exclusive activities in a way that maximizes fitness. Seasonal variation in activity budgets can be viewed as such an adaptive response.

The fundamental decision made by grazing wapiti is whether or not to feed. Although grazing animals generally respond to declining forage availability or quality by increasing foraging effort (Arnold 1964), there is a point where the marginal benefit obtained from feeding will be overshadowed by the marginal cost of obtaining food. This cost can be viewed energetically or in terms of increased risk of predation or decreased time available for other essential activities.

When engaging in activities such as resting, reproductive and social behavior, wapiti also must make decisions about which tactics to deploy. While resting, consideration must be given to site selection on the basis of suitability of local microenvironment and predatory risk, which posture to assume in order to conserve or dissipate body heat (Jacobsen 1973), and whether to sleep, be alert (Allison and Chicchetti 1976), or to ruminate.

In this chapter, I examine seasonal variations in the activities of wapiti over one annual cycle. The objective

was to document activity budgets in each season and to investigate the influence of selected environmental factors.

METHODS

Activity

Throughout one annual cycle the wapiti were observed during 3 to 24 hour observation sessions. To permit night observation, sessions were centered around the full moon although on many occasions a flashlight was used.

Records of the major activity of the herd, together with the number of individuals engaged in other activities, were made at 10-minute intervals. Each 10-minute record was based on the predominant activity of an individual animal during the immediately preceding 10-minute period. The major activities recorded were: 1) foraging, 2) resting (lying or standing), and 3) minor activities such as walking, running, drinking, sparring courtship, maternal care, auto- and allo-grooming, and barkstripping.

When there was adequate light, resting was recorded as either resting or resting ruminating. Feeding was recorded as either grazing or browsing and notes were kept on forage selection. Although diet selection was not systematically quantified, an overview of seasonal shifts in food habits was obtained.

Index of Diet Quality

Relationships between fecal nitrogen and forage digestibility and intake have been investigated by a number

of workers and have been reviewed by Hutchinson (1958) and Coop and Hill (1962). It was first shown by Raymond (1948) and Lancaster (1949) that herbage digestibility was positively related to the nitrogen concentration in feces. Several regression equations have since been developed for domestic sheep which permit digestibility to be predicted from a knowledge of %N in feces (Coop and Hill 1962, Lambourne and Reardon 1963). Similarly Hebert (1973) developed equations for two groups of Rocky Mountain bighorn sheep (*Ovis canadensis*).

The nitrogen in feces consists of undigested dietary N, bacterial N and metabolic N from gastrointestinal secretions and epithelial sloughage. The contribution of these components varies with feed characteristics (digestibility and N content) and intake (Hutchinson 1958). Despite its variable composition feces N concentration is highly correlated with feed digestibility. The strength of this relationship is evident from correlation coefficients demonstrated by a number of workers: r^2 = .78 and .68 (Hebert 1973), .83 (Lambourne and Reardon 1973) and .92 to .97 (O'Donovan *et al*. 1967).

On the strength of the correlation between feces N and feed digestibility, feces crude protein concentration (N x 6.25) was used as an index of temporal shifts in diet quality throughout the present study. Fresh feces were collected on an average every 15 days and were stored by freezing until analysis. Sample sizes ranged between 1 and

12 and averaged about 6. Nitrogen was determined using the macro-Kjeldahl method (A.O.A.C. 1965).

Movements

The central location of the herd was recorded at each 10-minute interval during continuous foraging bouts using x-y coordinates on 25 by 35 cm aerial photographs. This permitted determination of distances travelled during foraging. Straight line distances between 10-minute points were summed and the rate of travel was calculated in meters per hour of feeding.

Description of the Environment

Notes were kept on the initiation and chronology of growth of grasses, forbs and woody plants. Snow depth was measured with a meter rule and notes were kept on crusting and melting rates throughout the study area.

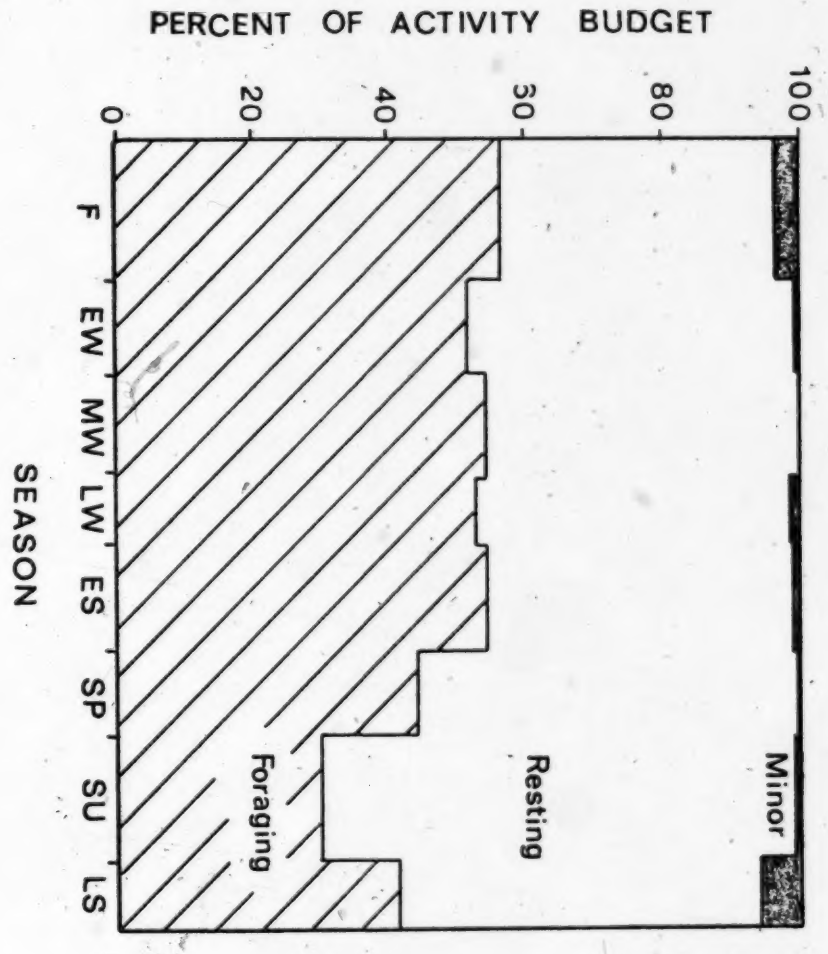
RESULTS

Seasonal Activity Budgets

Foraging and resting were the most time-consuming activities in all seasons (Fig. 2.1). Together they constituted no less than 94% (in late summer) of the total observations and averaged 98.3% over all seasons. Minor activities tended to be sporadic and/or seasonal in occurrence and together contributed less than 5.4%. Minor activities included sparring, courtship, maternal care, auto- and allo-grooming, and barkstripping.

Foraging and resting were largely antithetical in

Figure 2.1 Percent frequency of foraging, resting and minor activities of wapiti in each season of the study.


PERCENT OF ACTIVITY BUDGET
0
20
40
60
80
100
F
EW
MW
LW
ES
SP
SU
LS
SEASON
Foraging
Resting
Minor
F Fall
EW Early Winter
MW Mid Winter
LW Late Winter
ES Early Spring
SP Spring
SU Summer
LS Late Summer

nature such that when wapiti were not resting they usually were foraging. Thus, the activity budget could be summarized adequately by consideration of foraging time alone.

Time spent foraging varied significantly through the seasons (Table 2.1). It contributed 56.8% in the fall, then decreased during the winter periods. Foraging increased marginally again in early spring to 54.4% when much of the study area was essentially snow free.

The spring flush of vegetation in May was accompanied by a marked decline in foraging activity. A further decline occurred in summer when foraging contributed only 29.9% to the activity budget, the lowest value for any season. By late summer foraging time increased again to 41.3%.

Foraging Tactics

Grazing and browsing are two major foraging tactics. Grazing was defined as foraging in the field layer on grasses, grasslike plants and forbs. Browsing was defined as foraging on twigs and foliage of shrubs and trees.

The two major environmental factors which influenced foraging behavior were plant phenology and snow conditions. These factors affected the availability, quality and distribution of food items.

Following leaf abcission from woody plants in late September, wapiti fed predominantly in the field layer. They were obviously selective in what they consumed; green leafy material was preferred over stems and dead material. Grasses predominated in the diet. Forbs, particularly the leaves of

Table 2.1. Seasonal frequencies of foraging.

Season	Activity frequencies: Foraging	All other Activities	Total	%Foraging
Fall	2807	2136	4943	56.8
Early Winter	1424	1343	2767	51.5
Mid Winter	1395	1183	2578	54.1
Late Winter	1567	1399	2966	52.8
Early Spring	1502	1259	2761	54.4
Spring	2038	2576	4614	44.2
Summer	1795	4143	5908	29.9
Late Summer	414	588	1002	41.3
Total	12942	14597	27539	47.0

Chi Square = 1089.3 with 7 degrees of freedom (P<.01)

Homogeneous subsets are underlined (P<.05)

Fall	Early Spring	Mid Winter	Late Winter	Early Winter	Spring	Late Summer	Summer

equality of two proportions tests (Sokal & Rohlf 1969)

dandelion and vetch, were preferred. However, the abundance of these plants was low and declined steadily with recurring frosts. By the end of October green plant material became scarce. Dried erect forbs such as Canada thistle and common nettle were consumed as was bunchberry (*Cornus canadensis*). In the meadows wapiti appeared to select for green grass leaves. When browsing, the wapiti consumed little woody material; rather they selected leaves which had cured but not fallen from the stems.

With the development of permanent snow cover in late November, browsing increased. Twigs of woody plants were the major components of browse consumed although dried leaves retained on branches were eaten whenever encountered. However, grazing still dominated. Snow cover remained light through December (less than 20 cm) and the wapiti were able to procure herbage by pushing the snow away with their muzzle as they grazed. Pawing was infrequent. There still appeared to be an element of selectivity while grazing although green herbage was scarce.

With the arrival of deep snow cover (35 cm and greater) in late December, browsing increased. The nature of the snow pack during January and the first half of February demanded considerable effort to dig feeding craters. The snow was deep, ranging up to 45 cm, and tended to fall into the crater as it was excavated, making exposure of herbage difficult. Once herbage was exposed, it was thoroughly and non-selectively consumed.

Woody plant material was the major dietary component during mid winter. Aspen and beaked hazel appeared to be the most important browse species in the diet and were the most abundant browse species in the poplar forest. Saskatoon appeared to be next in importance. Willow occassionally was used but seemed to be of minor importance despite its abundance. Chokecherry, pin cherry and balsam poplar were consumed in minor amounts. Although dogwood was not abundant, it was consumed whenever encountered, particularly the current annual growth of twigs. When feeding on dogwood shrubs which had previously been browsed, the wapiti would consume stems up to 6 mm in diameter. The wapiti were never observed eating twigs of raspberry, rose or snowberry.

With the appearance of open patches in late February and early March, grazing again predominated and was focused on the open meadows. Although this shift was likely due to increased availability of herbage, snow conditions in the forest may have also been a determinant. The warm weather resulted in crusting and increased snow density. The crust in the deep snow in the forest may have impeded movement and wapiti did not venture into deep snow unless the ambient temperature was sufficiently high to cause softening of the crust.

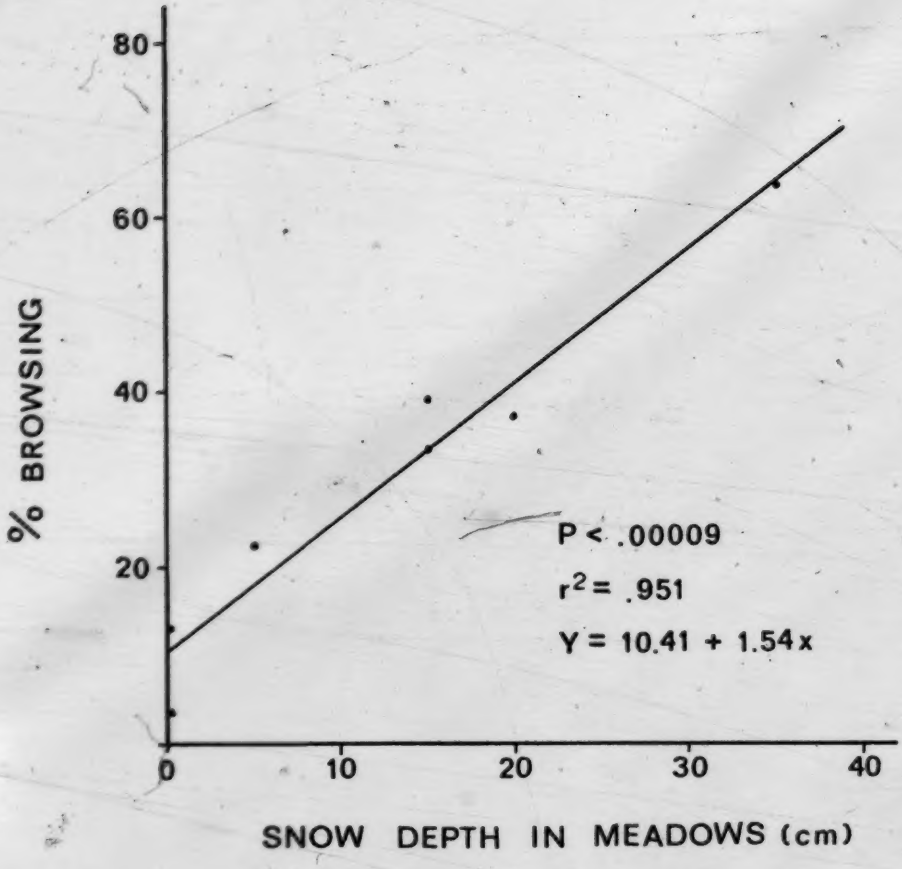
Cratering was also difficult in the dense snow pack unless it was softened by warm conditions. When ambient temperatures were above freezing, pawing through the 10 cm snow cover appeared easy and the granular snow was often

simply pushed aside with the muzzle. However, with freezing temperatures which usually occurred at night, the snow cover became extremely hard making excavation difficult. Grazing in the patches of exposed meadow was non-selective. The wapiti tended to consume wet freshly exposed herbage along the receding snow line surrounding open patches.

By the end of March, most of the snow disappeared from the meadows and ice cover in the wetlands began to melt. The wapiti appeared to be more selective in feeding again, selecting for grass leaves which remained green over the winter. Little browsing was done. About mid April, they began to feed on new sedge shoots in the wet meadows, the first available source of early growth. The relationship between browsing frequency as a percent of foraging time and snow depth in meadows is illustrated in Fig. 2.2.

Although grasses began to grow about April 25, they were not completely available until after the first week in May. The animals attempted to consume as much of this material as possible but cured, weathered grass made up a large proportion of the diet. By the 9th of May, the diet consisted largely of green plant material. During spring, the wapiti fed almost exclusively in the field layer. Grazing occupied 97.4% of the time spent foraging. Similarly, in the summer, grazing was the principal tactic (92.3%). Foraging emphasized forbs which were abundant from the end of May to the beginning of August. In late summer browsing assumed more importance (42.8% of time spent

Figure 2.2 Relationship between snow depth in meadows and percent frequency of browsing.


80
60
40
20
% BROWSING
P < .00009
r² = .951
Y = 10.41 + 1.54x
0
10
20
30
40
SNOW DEPTH IN MEADOWS (cm)

foraging) coinciding with a decrease in the abundance of forbs and advancing maturity of grasses. Both leaves and terminal portions of current growth twigs were consumed.

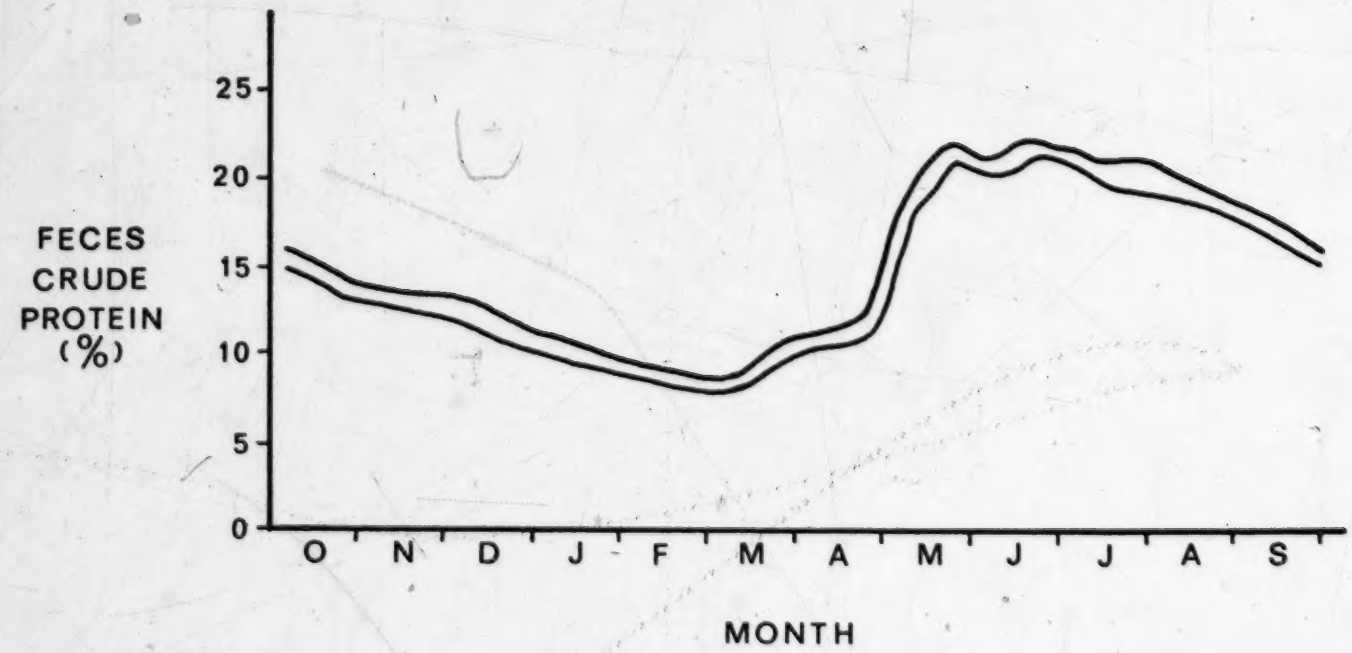
Diet Quality

Changes in diet quality, as indicated by feces crude protein content, paralleled observed changes in the quality of the diet selected. The seasonal pattern in feces crude protein is illustrated in Fig. 2.3.

Feces crude protein gradually declined through the fall reflecting the declining quality of available feed and decreasing selectivity. Diet quality apparently reached a low in late February and early March when the wapiti were feeding non-selectively on weathered herbage in patches of exposed meadow. The crude protein content of hand picked grasses from these patches was 7.1%.

During the period in late March and early April when the meadows were largely snow free, feces crude protein rose from 8.5% to 10.7%. This agrees with a subjective observation of increased selectivity compared to early March. Feces collected on April 25 had a mean crude protein content of 11.9%. This increase likely reflected the increasing availability of sedge and grass shoots, the only green material available. Sedge shoots collected at that time contained ony 9.2% crude protein while grass shoots contained 17.0% crude protein. Although grasses initiated growth by April 25, they evidently did not contribute much to the diet until they achieved sufficient length in early

Figure 2.3 Annual pattern of crude protein content (%) of wapiti feces. Standard errors either side of the mean are joined by a line.


FECES
CRUDE
PROTEIN
(%)
25
20
15
10
5
0
O
N
D
J
F
M
A
M
J
J
A
S
MONTH

May. By May 10 the diet consisted largely of early growth plant material and feces crude protein had risen to 18.9%.

Diet quality remained high throughout the remainder of May, June and early July, with crude protein contents averaging about 21%. Declining diet quality was evident after the end of July. This continued until the end of September when the last samples were collected. This was interpretable in terms of changes in the abundance of forbs, maturation of grasses and eventually, in September, abcission of leaves from trees and shrubs.

Rates of Travel during Foraging

Mean rates of travel during feeding bouts changed throughout the year (Table 2.2). The lowest rate of movement (63 m/hr.) occurred during late February to early March at a time when wapiti largely restricted their foraging activity to small patches of exposed upland meadow. Conversely, the greatest rate of movement occurred during summer (302 m/hr.), a period of great abundance of high quality feed.

Rates of travel for spring through late summer were similar while the periods from fall to early spring fell into a significantly different group. These two sets respresented a period of abundant high quality feed, and a period of declining or poor feed availability, respectively.

Resting Behavior

Considered as resting were lying, lying ruminating, standing idle, and standing ruminating. Standing ruminating was observed only infrequently; it was of short duration,

Table 2.2. Rates of travel during foraging bouts in each season.

	Season							
	Spring	Summer	Late Summer	Fall	Early Winter	Mid Winter	Late Winter	Early Spring
Mean rate of travel (m/hr.)	266	302	241	105	91	66	63	88
Standard Error	20	31	29	24	33	11	11	13
Sample size	20	18	7	20	8	9	11	12

Analysis of variance F=30.56, df=7, P<.001

Student-Newman-Keuls Classification

Summer	Spring	Late Summer	Fall	Early Winter	Early Spring	Mid Winter	Late Winter

and usually preceded a bout of lying ruminating. Sleeping was infrequent and lasted no longer than 10 or 15 minutes. Characteristically rumination occurred in a sternal recumbent position, although it was also observed during lateral recumbancy with the legs out but the head held upright.

Seasonal contributions of rumination to the activity budget are presented in Table 2.3 for all but the early winter and late summer periods for which adequate data were not collected. Rumination was greatest in winter. In other seasons when foraging became more selective, rumination declined.

Herd Stability

Herd cohesion, defined as the proportion of the total number of wapiti under observation at each 10-minute interval, varied seasonally ($P < 0.001$). During the fall and winter periods herd stability was high, ranging between 0.96 and 0.99 (Table 2.4). Fragmentation occurred to an extent during the rut in October when the dominant bull forced oestrus cows to leave the main group. In spring and summer, the wapiti became less gregarious and on the average about 25% of the animals were absent from the main group. Individuals frequently were found alone engaging in independent activities.

Parturition in the latter half of June resulted in the seclusion of parous cows. Although these animals joined the herd about a week after giving birth, they were committed to

Table 2.3 Seasonal contributions of rumination to the activity budget of wapiti.

Season	Number of Resting Observations	Proportion Ruminating	Percent of Total Activity Budget
Fall	883	0.56	22.3
Winter	760	0.81	37.7
Early Spring	994	0.59	21.4
Spring	1076	0.41	22.7
Summer	1430	0.28	19.4

Table 2.4 Herd stability through an annual cycle.

	Season						
	Fall	Early Winter	Mid Winter	Late Winter & Early Spring	Spring	Summer	Late Summer
Mean Herd Stability	.96	.99	.97	.95	.75	.74	.69
Standard Error	.09	.03	.07	.09	.24	.19	.10
Sample Size	576	309	294	507	676	887	214

feeding their calves at about six-hour intervals. Since the calves remained in hiding until they were two to three weeks of age, this meant that the cows had to leave the herd periodically.

DISCUSSION

The seasonal activities of wapiti were influenced by a number of physical and biotic environmental factors, particularly changes in the forage base. Generally, as forage quality and availability declined the amount of time allocated to foraging increased. This response is characteristic of domestic herbivores (Tribe 1955, Arnold 1964). Jarman and Jarman (1973) observed that impala (*Aepyceros melampus*) increased feeding time on poor pasture and similar results have been noted for buffalo (*Syncerus caffer*) (Grimsdell and Field 1976, Lewis 1977).

In this study, wapiti spent the least amount of time foraging in summer when high quality forage was most abundant. As plants matured in late summer and fall, foraging times increased. Diet quality, as reflected in feces crude protein, declined throughout the winter. In early spring, allocation of time to foraging rose abruptly, reaching a peak in the annual cycle; diet quality improved moderately. When early growth vegetation became abundant in May, foraging time again declined.

The strategic nature of the seasonal shifts in foraging time can be understood when the activity budget is viewed as

a process of optimization. In this context, a strategy refers to the ways in which time and energy are allocated, and optimization refers to a process whereby time and energy are deployed in a manner which results in the greatest net benefit to the animal. The constructs of the 'Optimal Foraging Theory' were first outlined by Emlen (1966) and McArthur and Pianka (1966) and have since been applied in analysing foraging behavior of a range of animal taxa (Pyke *et al* . 1977). In general terms, optimization involves choosing a currency, selecting an appropriate cost-benefit function, and finally solving for the optimum.

There are a number of currencies which could be important to a herbivore. For example, susceptibility to predation or breeding success may depend on decisions of whether or not to engage in an activity. However, for the purpose of this discussion, energy is most appropriate. The cost-benefit function would be the relationship between the useful energy derived from a food item less the cost of procurement, expressed as a function of the time it takes to obtain and handle (find, ingest and digest) the item. The animal can achieve an optimum by selecting items in proportion to their net rate of energy profit and by appropriate allocation of time (Pyke *et al* . 1977). Without precise simultaneous measures of the energetic value of each item in the diet and the energy required to obtain and handle it, it is impossible to deal with this question quantitiatively. However, optimal foraging theory does

provide a useful framework for interpreting observed patterns.

Theoretically, an animal can pursue two basic strategies. The *energy maximization* strategy hypothesizes that fitness is maximized when the net rate of energy intake for a set feeding time is maximized (Emlen 1973). Presumably this would occur when the time available for foraging is limited by the necessity of engaging in other activities. Alternatively the strategy could be one of *time minimization* in which maximum fitness is associated with minimizing the amount of time spent satisfying energy demands (Schoener 1971). In this case, time spent foraging would be limited by nutritional requirements rather than the time required for other activities.

Wapiti appeared to engage in both of these strategies, though at different times of the year. During the spring, summer, and later summer when good quality forage was readily available the wapiti attempted to minimize the amount of time needed to consume forage which would meet their requirements for growth, fattening, lactation, etc. By employing this strategy they were able to minimize activity during periods of the day when the energy cost of foraging or physical discomfort would have been increased due to thermal conditions or insect harassment (Chapter III). The efficiency of foraging would therefore be enhanced by restricting feeding to only the most favorable periods. The greater allocation of time to resting in the spring and

summer can also be viewed as a growth promoting strategy since the energy conserved by restricting activity would be available for growth.

In the fall, as the abundance of high quality items declined, the wapiti responded by increasing foraging time. Craighead *et al* . (1973) also noted that Yellowstone Park wapiti increased time spent foraging from summer to the fall. Increases in foraging time in response to declining abundance of high quality items provides an opportunity for greater selectivity and probably allows diet quality to remain higher than if foraging time had not been altered. Emlen (1966) postulated that consumers should become more selective as food density increases. Although food habits were not specifically quantified this appeared to be the case, for the wapiti specialized on grass shoots in the spring and forbs in the summer and dietary expansion appeared to occur as the abundance of high quality items declined through the late summer and fall.

The observed differences in distances travelled while foraging can also be seen as a tactical change related to foraging conditions. During periods when high quality forage was abundant, animals travelled greater linear distances while foraging than during periods of scarcity. This may have reflected the intensity of searching for acceptable food items such that during periods of abundance search intensity was low and less time was spent travelling a set distance than when preferred items were scarce and search

intensity was high. Similarly, Novellie (1978) found that the amount of time spent at a feeding station by springbok (*Antidorcas marsupialis*) and blesbok (*Damaliscus dorcas phillipsi*) was inversely correlated with forage quality.

The maximum amount of time spent foraging was 56.8% and this compares favorably with the maximum value (54%) reported for wapiti in the spring in Yellowstone National Park by Craighead *et al* . (1973). This limit may be a function of diet quality or digestibility which largely controls the rate of passage of digesta and hence amount consumed by a ruminant (Baile and Forbes 1974). Once diet quality fell below a critical point, increases in foraging time may have been constrained by the rate of digestion. In both late fall and early spring, feces crude protein was close to 11.5%. This index value may indicate a minimum level of diet quality where forage digestibility and rate of passage are still sufficiently high to permit a maximum amount of time for foraging.

Since rumination serves to reduce particle size, it is not surprising that high fiber forages such as the winter diet would result in an increase in time spent ruminating. This response was obvious in the winter period when ruminating comprised 37.7% of the activity budget compared with 19 to 22% in other seasons.

Where time available for foraging is limited, as in winter, a shift in strategy to energy maximization apparently occurred. In employing this strategy, an animal

maximizes energetic profit from forage by achieving the optimal balance between energy acquired from the forage and energy expended in foraging. The tactical shifts evident in changes in feeding style in relation to snow conditions may reflect energetic optimization. Under the influence of declining forage availability, the quality of the diet fell through the winter reaching a low when crusting conditions in the forest inhibited movement and grazing was limited to a few small snow free patches in the meadows.

The consequence of further reductions in forage availability is speculative. Although the time spent foraging remained relatively constant through the winter in this study, observations on Yellowstone Park wapiti (Craighead *et al* . 1973) indicated scarcity of forage can result in a marked reduction in foraging time. In that study, foraging occupied only 38.5% of the winter activity budget while resting and bedding occupied 57.9%. Thus, the relationship between foraging time and forage availability may be parabolic. As forage availability declines from high to moderate, foraging time increases. Under slightly impoverished conditions, foraging is deployed for a maximum amount of time under the constraint of physical gut fill. Further limitation of forage availability makes resting a more energetically favorable activity than foraging.

The time minimization strategy exhibited by the wapiti in summer contrasts with the foraging strategy of moose reported by Belovsky (1978). Apparently moose pursue the

alternate strategy of energy maximization during the summer. The difference between the two species may be related to contrasting feeding styles and the effect that this has on high quality forage available for body growth. The period for body growth and energy deposition in moose coincides with the time between leaf flush in browse plants (mid May) and leaf abcission (beginning of October) (Stewart *et al* . 1977). This is a consequence of the morphological and physiological specialization of moose for feeding on browse.

In contrast, wapiti begin to feed selectively in the spring soon after the first green vegetation is evident in the field layer and possibly earlier. Diet quality remains relatively high late into the fall. This is a consequence of the versatility of the species; it is a generalist herbivore while the moose is a specialist.

The period for positive energy balance in moose in the boreal forest was estimated to average about 140 days (Stewart *et al* . 1977) while for wapiti the period of weight gain maybe as long as about 234 days (Ch. 5). If the objective of summer feeding is to achieve a level of body growth and tissue energy storage which will ensure reproductive success and over-winter survival, then the moose has a shorter time in which to meet this objective than wapiti. It is expected that the moose will gain weight more rapidly than the wapiti during this period. It follows that the moose would make best use of its time in the summer growth period by foraging as much as possible, subject to

the constraint of time required for other activities. Moose can therefore be expected to spend more time foraging than wapiti and the time available for foraging will be more limiting for moose than for wapiti in the summer.

The reduction in foraging time in early, mid and late winter likely was based on optimization of energetic criteria including declining forage quality, reduced availability due to snow conditions, and increased costs of procuring food and thermoregulation. However it is also important to recognize the role of endogenous or periodic physiologic factors which could regulate or influence the level of activity in different periods of the year. Seasonal variations in food consumption and feeding activity of wild ruminants not correlated with food quality or availability, have been reported (Ozoga and Verme 1970).

The metabolic basis of this behaviour is indicated by a number of studies on white-tailed deer. Silver *et al.* (1969) detected a lower metabolic rate in winter than during summer and Holter *et al.* (1976) reported seasonal differences in the equations for estimating metabolism from heart rates. Seal *et al.* (1972) demonstrated decreased serum thyroxine levels and decreased metabolic rates in white-tailed deer in the winter. Caribou and reindeer (*Rangifer tarandus*) have also been shown to voluntarily reduce caloric intake by 35 to 40% in the winter (McEwan and Whitehead 1970). Reduced metabolic requirements during the period when resources are scarce and when thermal conditions may be adverse would

permit a reduction in expenditure of energy for foraging and facilitate energy maximization.

Seasonal variability in physiologic requirements may also be important in determining the amount of time an animal allocates to foraging during periods of greater forage abundance. The added demands of late pregnancy and lactation have been shown to result in comparatively greater foraging times in domestic sheep (Arnold and Dudzinski 1967), waterbuck (*Kobus defassa*) (Spinage 1968) and impala (Jarman and Jarman 1973).

The temporal nature of the forage resource was a major cause of variation in social behavior. Individuals tended to be less gregarious during the spring and summer than during fall and winter. Aggregation during the latter periods can be interpreted as both an antipredator strategy and a feeding strategy. During periods when foraging time is at a premium, any factor which enhances the efficient use of that time for foraging is strategically valuable. A wapiti feeding in the company of others has the advantage of saving time spent watching with an increase in time spent foraging. When time available for feeding is limited, aggregation plays an important role in maximizing energy intake and at the same time minimizing the risk of predation. Since relatively less time is spent foraging in the summer, relatively more time can be spent watching. If feeding must occupy a greater proportion of time, then the minimum group size required for safety must be greater (Geist 1979).

Dispersal and independence of herd members during the spring and summer results in a reduction in intraspecific contact and would tend to enhance growth and energy storage by permitting the individual to rest and feed at leisure without social pressures. In contrast, aggregation during the winter results in conflicts over limited resources but this disadvantage would be offset by a reduction in predatory risk. It is also possible that summer dispersal may have been a function of cover density. Dasman and Taber (1956) noted that cervids often form small groups or are solitary when dense cover is inhabited and larger groups are typical in open areas of grasslands and tundra. Seasonal changes in the quality of cover in a deciduous forest are dramatic and may contribute to summer dispersal and winter aggregation.

Seclusion of the female at the time of parturition avoids social interactions at a time when she would be less able to respond appropriately to antagonistic herd members due to the stress of calving. Although parturient dispersal and hiding of neonates is a successful antipredator strategy (Lent 1974), it also may prevent intraspecific aggression. Although the hiding calf will cry loudly and bolt when frightened by the close approach of a strange animal, it is not fearful of conspecifics even when attacked. Further, the cow does not protect its calf from conspecifics; calves exposed to other wapiti before they have developed their behavioral and physical dexterity are often subject to abuse

if not mortality (Murie 1951, Harper *et al* . 1967, Kelly and Whateley 1975).

In conclusion, the strategies and tactics deployed by animals are the product of interaction between their physical, physiological and behavioral attributes and the constraints imposed by the environment. The wapiti is a highly versatile and successful species as evidenced by its opportunistic feeding habits (Kufeld 1973) and occupation of a wide range of biomes, from coastal rain forests (Harper *et al*. 1967), and semi deserts (McCullough 1971) to areas of unusual geographic characteristics such as thermal areas in Yellowstone National Park (Craighead *et al* . 1973).

Chapter 3

CIRCADIAN ACTIVITY PATTERNS

INTRODUCTION

Circadian activity patterns of most animals are the result of interaction between endogenous or physiological factors and environmental influences. A regular deployment of activities has been documented for many wild ruminants (Mitchell 1977, Walther 1973, von Berg 1978) including wapiti (Craighead *et al* . 1973, Collins *et al* . 1978). Reported activity rhythms are of two basic types: biphasic activity cycles with periods of peak activity at either end of the diurnal period and polyphasic patterns with 4 - 6 cycles within 24-hours.

One endogenous factor entraining such rhythms is energy balance or hunger and satiety. Lord (1964) suggested repletion-depletion cycles as the endogenous clock for regulating the daily activity pattern of rabbits and possibly other herbivores.

Changing light intensity also has been shown to entrain circadian rhythms. Hafez *et al*. (1969) noted that domestic herbivores are most active during periods of the day when lighting changes most rapidly. This pattern is shared by many wild ruminants which forage in crepuscular hours. However, Leuthold (1977) argues that this generalization is overly simplistic.

Numerous studies have shown that a variety of environmental factors other than illumination influence activity. Paramount among these is weather. The animal responds by altering its behaviour and/or seeking a more favorable microclimate. The manner in which the thermal environment affects behaviour varies with species-specific variation in body size, insulation, physiologic status and thermoregulatory mechanisms. Generally, activity is suppressed when it is hot or when it is very cold (Tribe 1955, Tester and Heegan 1965, Malachek and Smith 1976).

Within any season daily variations in cloud cover, wind, humidity and temperature can alter activity patterns. Chapman (1939) observed more deer feeding on cloudy than on clear nights and on calm rather than windy ones. In wapiti, bugling and rutting battles occurred to the greatest extent during cold evenings (Harper *et al.*, 1967).

Social factors influence individual activities through contagious behaviour or social facilitation. The consequence is that the activities of gregarious animals are often synchronized as individuals engage in the same activity as their neighbors (Jarman and Jarman 1973, Arnold and Dudzinski 1978)

This chapter identifies daily patterns of activity in wapiti at various times of the year and attempts to determine the extent to which these patterns are influenced by physical and biotic environmental factors.

METHODS

Activity Patterns

In periodic observation periods from September 1978 - October 1979, records were made of activity states at 10-minute intervals during periods of 6-24 hours in length. Each 10-minute record was based on the predominant activity of individual animals during the immediately preceding 5-minute period. In order to permit observations at night, study periods were centered around the full moon. The major activities recorded were: 1) foraging, 2) resting (lying or standing) and 3) minor activities.

In order to detect circadian patterns, all 10-minute observations were summed for half-hour intervals and expressed as percentages.

Individual activities for each 10-minute observation interval within each of 5 circadian time periods were compared during each season. These time periods were standardized in the following manner:

early morning:	the first 1/3 of the time interval between 0.5 hours before sunrise to noon;
morning:	end of early morning to noon;
afternoon:	the first 2/3 of the time interval between noon and 0.5 hours after sunset;
evening:	end of afternoon until 0.5 hours after sunset;

night: - the time interval between
0.5 hours after sunset and
0.5 hours before sunrise

The frequency of foraging within each time period was compared with an overall time adjusted mean (RTA) calculated for each season as follows:

$$RTA = \frac{T.F}{24}$$

where T is the length of a time period in hours and F is the percent frequency of foraging in that time period; the summation is for all five daily time periods.

Environmental Measurement

Every 10 minutes records were kept on solar radiation, ambient temperatures and wind. Solar radiation (Ly/min) was measured with a hand-held radiometer (Jochem 1976) and later transformed into watts/m^2. Wind velocity was subjectively rated on a scale of 0 to 5 and later assigned values of 0, 0.9, 2.7, 5.4, 8.9, and 13.4 m/sec corresponding to the scale. Insect harassment was rated on a 3 point scale; low, moderate and high. Notes were kept on plant phenology, precipitation and snow conditions.

Statistical Methods

The influence of weather on activity when the wapiti were in summer (May-Aug.) and winter (Sept.-Apr.) coats was analyzed by 'multivariate nominal scale analysis' (Andrews

and Messenger 1973). The data set was reduced by using only the predominant herd activity for each ten-minute observation. Activities were divided into two categories, mobile (grazing, browsing, walking) and stationary (bedding and standing). Independent variables describing the thermal environment (ambient temperature, solar radiation and wind velocity) were recorded as outlined in Table 3.1.

The data were also analyzed using multiple stepwise regression (Nie *et al* . 1975) for each season. The dependent variable was recorded as above but the three predictor variables were treated as continuous data.

RESULTS

Daily Activity Patterns

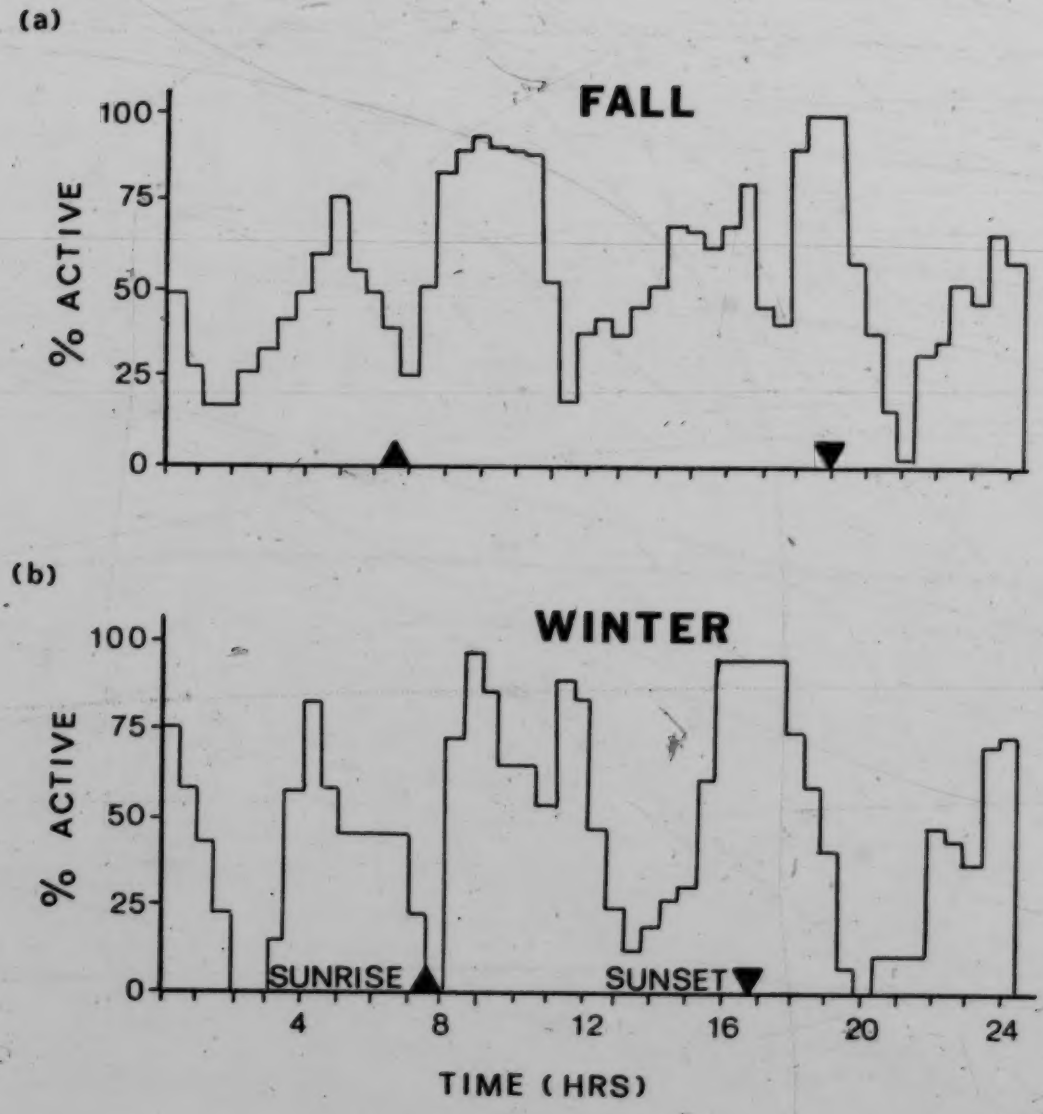
During fall and winter, feeding and resting alternated in a polyphasic manner over a 24-hour cycle (Fig.3.1a,b). During the spring and summer, the pattern was essentially biphasic with peak feeding periods at dawn and dusk (Fig 3.1c,d). In both fall and winter, peak resting occurred at sunrise with peak feeding one hour later. During mid-day the animals went through one or two feed-rest cycles. A major feeding period centered around sunset and in the winter continued for another hour and a half or more into darkness. Another feeding bout occurred at midnight in both fall and winter, then again a few hours before sunrise.

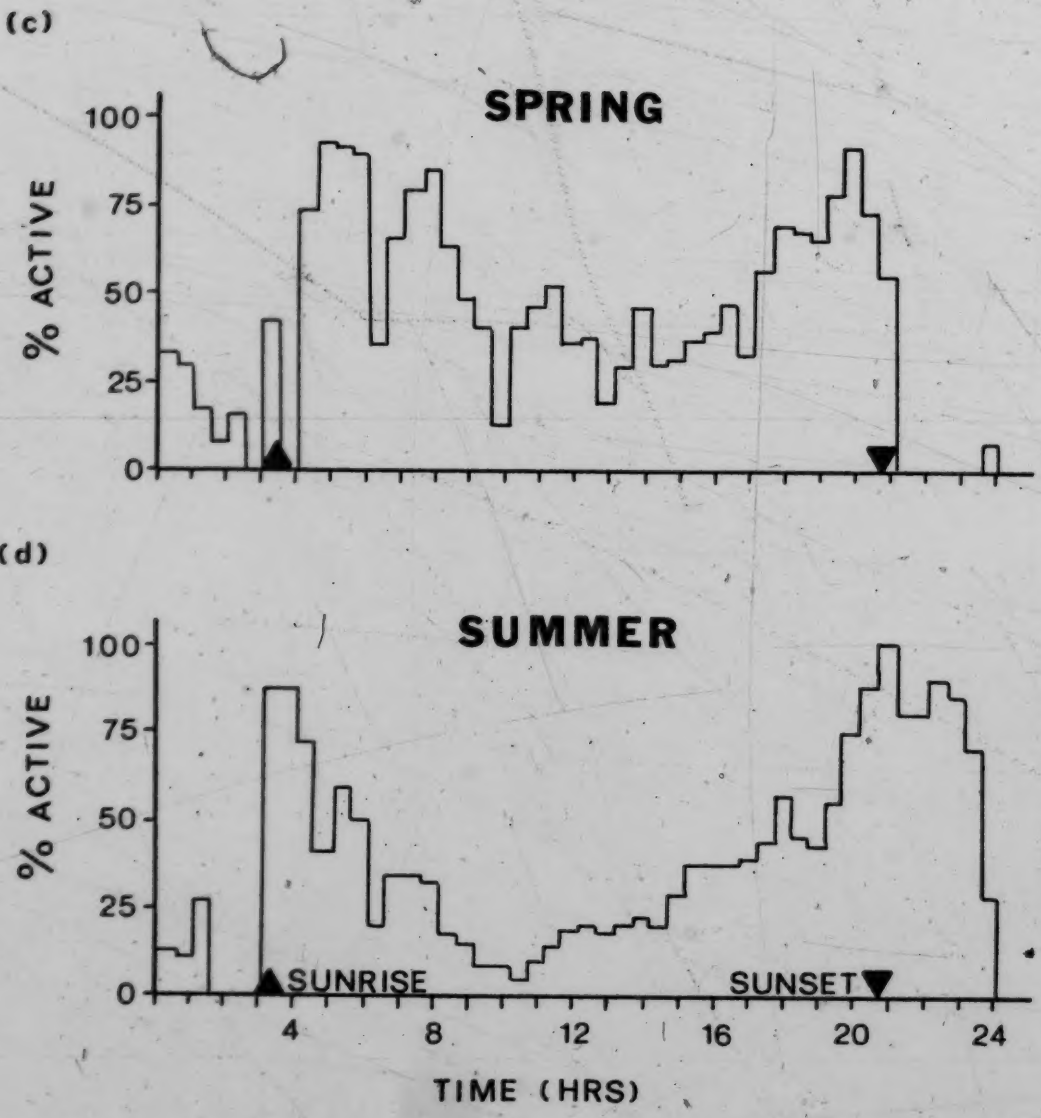
In spring and summer, feeding began about sunrise. Resting gradually replaced feeding as the morning progressed

Table 3.1 Categorical division of ambient temperature and solar radiation.

Category	Weather Variable	
	Ambient Temperature (°C)	Solar Radiation (W/m^2)
1	-35 to -25	0 to 14.0
2	-24 to -18	14.1 to 35.0
3	-17 to -11	35.1 to 56.0
4	-10 to -4	56.1 to 70.0
5	- 3 to 3	70.1 to 105.0
6	4 to 10	105.1 to 140.0
7	11 to 17	
8	18 to 24	
9	25 to 35	

Figure 3.1 Daily patterns of activity for each major season expressed as a percent of animals observed active in each 1/2 hour interval of the day.


(a)
FALL
100
75
50
25
0
% ACTIVE
(b)
WINTER
100
75
50
25
0
% ACTIVE
SUNRISE
SUNSET
4
8
12
16
20
24
TIME (HRS)


(c)
SPRING
100
75
50
25
0
% ACTIVE
(d)
SUMMER
100
75
50
25
0
% ACTIVE
SUNRISE
SUNSET
4
8
12
16
20
24
TIME (HRS)

reaching a peak during mid-day. This trend was reversed during the afternoon until shortly before nightfall when foraging was the dominant activity. In the spring, a major resting period began at nightfall and continued until sunrise the next morning. In contrast, during summer the evening foraging period extended well past sunset, until shortly before midnight.

Daily cycles of activity during early and late winter resembled the fall/winter pattern while the early spring/late summer patterns were transitional between winter/spring and summer/fall patterns.

Throughout the annual cycle the wapiti tended to be active in the early morning and evening (Table 3.2). Early morning foraging was least pronounced during fall and late winter. Morning foraging varied seasonally although there was a general tendency for a reduction from early morning to morning. Resting tended to be more prevalent in the afternoon. This behaviour was particularly pronounced in mid-winter. At that time, wapiti were observed 'basking' in the sun in exposed meadows. With few exceptions, the frequency of foraging during the night tended to depart little from the time-adjusted mean for this activity. The only notable exception occurred in spring when foraging occupied only 26% of the nocturnal activity budget.

Duration of Foraging and Resting Bouts

Foraging and resting bouts of individual wapiti were of variable duration (Tables 3.3,3.4). Frequently resting bouts

Table 3.2. Circadian distribution of foraging behaviour in each season.

Season		Time of Day: Early Morning	Morning	Afternoon	Evening	Night	Mean % Forage (Time Adjusted)
Fall	% Forage	53.9	68.0	50.8	62.3	47.1	53.1
	N	332	1707	1263	345	1296	
Early Winter	% Forage	97.3	42.2	54.5	52.6	48.6	51.7
	N	185	678	457	152	1295	
Mid Winter	% Forage	69.0	72.2	31.4	86.5	49.1	53.4
	N	87	468	714	348	961	
Late Winter	% Forage	41.2	59.6	44.0	69.3	49.7	51.3
	N	187	899	1021	398	461	
Early Spring	% Forage	69.6	54.8	39.4	79.9	54.8	55.7
	N	161	977	1014	483	126	
Spring	% Forage	78.0	54.2	36.3	65.6	25.8	45.5
	N	50	769	2108	961	726	
Summer	% Forage	59.3	21.0	24.4	55.8	49.1	38.2
	N	221	1438	3227	649	373	
Late Summer	% Forage	60.5	28.9	22.7	47.5	50.4	39.7
	N	76	194	172	322	238	

Table 3.3. Feeding bout duration in each season.

	Season							
	Spring	Summer	Late Summer	Fall	Early Winter	Mid Winter	Late Winter	Early Spring
Mean Duration (hours ± S.E.)	1.9 ±.13	1.2 ±.08	1.9 ±.08	2.9 ±.22	2.0 ±.11	2.2 ±.13	2.5 ±.12	2.1 ±.12
Sample size	118	97	27	21	45	65	92	99

Analysis of variance F=14.78 df=7,556 P<.0001

Student-Newman-Keuls classification

Summer	Spring	Summer	Winter	Spring	Winter	Winter	Fall

Table 3.4. Resting bout duration in each season.

	Season							
	Spring	Summer	Late Summer	Fall	Early Winter	Mid Winter	Late Winter	Early Spring
Mean Duration (hours ± S.E.)	2.5 ±.19	4.6 ±.27	3.1 ±.25	1.8 ±.16	2.5 ±.12	2.7 ±.16	2.0 ±.13	2.25 ±.11
Sample size	105	92	24	13	54	52	78	82

Analysis of Variance F=20.63 df=7,492 P<.0001

Student-Newman-Keuls classification

Summer	Late Summer	Mid Winter	Spring	Early Winter	Early Spring	Late Winter	Fall

were broken by short feeding bouts during which the animal would rise from its bed, stretch, defecate, graze for several minutes then lie down in another location. This sequence of activities, though recorded as foraging, was not included in this analysis. A resting or foraging bout was defined as a period of constant activity which lasted for 20 minutes or longer.

Seasonal variations in the duration of feeding bouts were marked. On average foraging bouts were shortest during the summer (1.2 hours) and longest during the fall (2.9 hours). Durations in the other seasons ranged from 1.9 to 2.5 hours.

The initiation and termination of bouts of feeding and resting was particularly difficult to determine during June and July. During that time, wapiti frequently interrupted resting periods by feeding while bedded. These feeding periods were usually short making it difficult to assess if a resting bout had ended or a feeding bout had begun. The occurrence of this feeding style coincided with a period of abundant nutritious forage.

Synchronization of Activity

Individual animals tended to conform to the modal activity of the group. In this study the degree of synchronization was determined by expressing the number of animals engaged in the same activity as a proportion of the total number under observation. Mean values for this parameter are presented in Table 3.5 for each of the four

major seasons. Data were pooled for early, mid and late winter and early spring (winter); and for summer and late summer (summer). Synchronization of activities was high, ranging from 84 to 91%.

Environmental and Biotic Determinants of Activity

Temperature, radiation, wind and precipitation are major components of the thermal environment. In response to adverse thermal regimes animals could elect to seek shelter, alter activity patterns or both. The results in this section deal with the effects of weather on activity.

The low generalized R^2 values for winter (0.04) and summer (0.08) coats indicated that the thermal environment explained relatively little of the variation seen in wapiti activity in relation to pelage type (Table 3.6). This suggests the underlying importance of other factors.

The relative importance of temperature, solar radiation and wind are indicated by the generalized eta-square values. Changes in activity with ambient temperature and solar radiation are illustrated in Figs. 3.2 and 3.3.

In winter coat ambient temperature exerted a greater influence on activity than solar radiation. This is also suggested by Fig. 4 in which mobile activities decreased much more slowly in winter coat than in summer coat as solar radiation increased. The marked decrease in mobile activity in summer coat as solar radiation increased agrees with the observed decline in mid-day activity during the spring and summer months.

Table 3.5 Synchronization of activities in each major season.

	Fall	Winter	Spring	Summer
Mean	.859	.840	.909	.894
Standard Error	.007	.008	.006	.006
Sample size	576	1110	676	1101

Figure 3.2 Changes in activity (%) in relation to ambient temperature and seasonal coat type. Sample size is indicated in parenthesis.

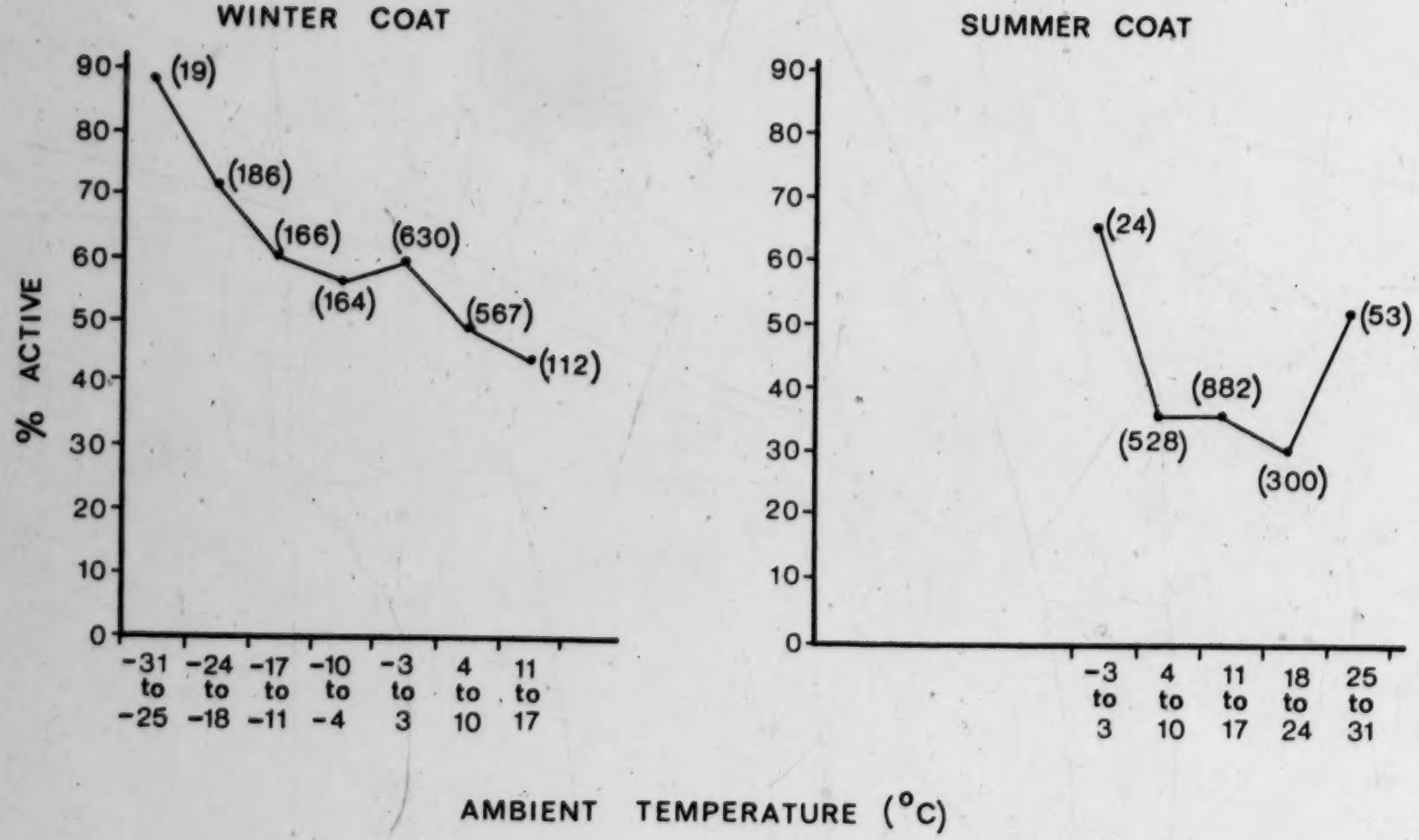

WINTER COAT
SUMMER COAT
% ACTIVE
90
80
70
60
50
40
30
20
10
0
(19)
(186)
(166)
(164)
(630)
(567)
(112)
(24)
(528)
(882)
(300)
(53)
-31 to -25
-24 to -18
-17 to -11
-10 to -4
-3 to 3
4 to 10
11 to 17
-3 to 3
4 to 10
11 to 17
18 to 24
25 to 31
AMBIENT TEMPERATURE (°C)

Figure 3.3 Changes in activity (%) in relation to solar radiation and seasonal coat type. Sample size is indicated in parenthesis.

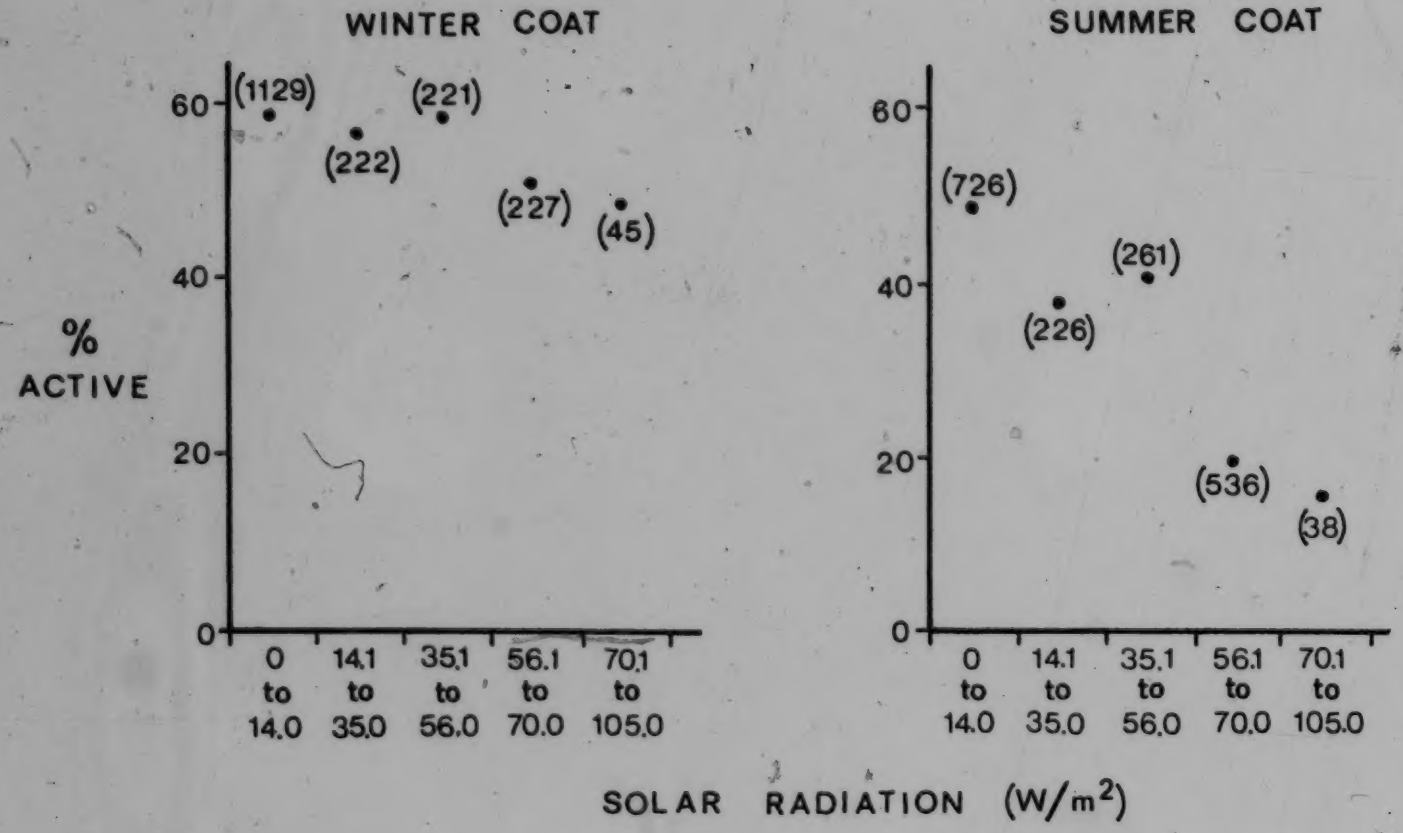

WINTER COAT
SUMMER COAT
% ACTIVE
60
40
20
0
(1129)
(222)
(221)
(227)
(45)
(726)
(226)
(261)
(536)
(38)
0 to 14.0
14.1 to 35.0
35.1 to 56.0
56.1 to 70.0
70.1 to 105.0
SOLAR RADIATION (W/m²)

Table 3.6 Analysis (MNA)* of the effects of ambient temperature, solar radiation and wind velocity on activity in winter and summer coats.

	Generalized Eta²			
Coat type	Ambient Temperature	Solar Radiation	Wind Velocity	Generalized R^2
Winter	0.0279	0.0034	0.0077	0.0355
Summer	0.0112	0.0653	0.0098	0.0786

*Multivariate Nominal scale Analysis

As ambient temperature increased from -31 to +17°C, mobile activities of animals in winter coat decreased from 90% to 45%. The response to ambient temperature in summer coat was paradoxical since the percent of mobile activities remained relatively constant between 4 and 24°C but increased markedly below and above that range. The increase in mobile activities at the lowest temperature range (-3 to +3°C) likely represented an increase in foraging to offset higher thermoregulatory costs. The increase at the hottest environmental temperatures appeared to be caused by an increase in harassment by biting insects.

Influence of Weather on Activity in Each Season

During the fall, temperature and solar radiation both had significant effects on mobile activities (Table 3.7). While increasing ambient temperature reduced activity, solar radiation tended to have the opposite effect. The explanation for this apparent incongruity may lie in the ability of the wapiti to choose more favorable microenvironments, i.e. shade. Together ambient temperature and solar radiation explained 8.5% of the variance in fall activity.

The mean temperature during observation periods in the early winter declined to -6.1°C from 0.8°C in the fall (Table 1.2). Likewise mean solar radiation declined from 21.8 to 5.4 W/m^2. Consequently, it is not surprising that wind appeared to depress mobile activities more in winter than in fall. Very little of the overall activity was

Table 3.7. Multiple stepwise regression between activity and meteorological variables.

Season	Statistic	Independent Variables: Ambient Temperature	Solar Radiation	Wind Velocity	Sample Size	Multiple R^2
Fall	B	-0.016	0.002	0.006	576	0.085***
	R^2 change	0.075***	0.010*	0.000		
Early Winter	B	0.002	0.001	-0.032	309	0.017
	R^2 change	0.001	0.001	0.016*		
Mid Winter	B	-0.024	-0.003	-0.037	294	0.164***
	R^2 change	0.123***	0.018*	0.023**		
Late Winter	B	-0.002	-0.001	0.004	350	0.004
	R^2 change	0.000	0.002	0.001		
Early Spring	B	-0.003	-0.007	-0.036	315	0.119***
	R^2 change	0.000	0.053***	0.065***		
Spring	B	-0.003	-0.002	0.053	686	0.017**
	R^2 change	0.001	0.010**	0.006*		
Summer	B	0.011	-0.005	-0.028	886	0.105***
	R^2 change	0.013***	0.090***	0.002		
Late Summer	B	0.012	-0.005	-0.450	214	0.046*
	R^2 change	0.007	0.025*	0.014		

* P<.05 ** P<.01 *** P<.001

explained by wind velocity (1.6%) and neither of the other variables had significant effects. Considered together the three weather variables had no significant effect on activity in fall and early winter.

In contrast, all three variables exerted significant influences on activity during mid winter. Ambient temperature had the most important effect. Again mobile activities declined as temperature increased. Similarly, increasing solar radiation decreased activity since wapiti tended to 'bask' in the afternoon sun. Wind reduced activity. Overall, 16.4% of the variation in mid winter was explained by temperature, radiation and wind.

In late February and early March (late winter), temperatures warmed considerably compared to the mid winter period. This is seen in both mean temperature and solar radiation (Table 1.2). On average this period was more windy than any other. These conditions had no detectable effect on activity.

In the early spring, weather explained 11.9% of the variation in activity. Both solar radiation and wind depressed activity while temperature had no effect.

Though significant ($P<.01$), the influence of the three weather variables was very small in the spring ($R^2 = 0.017$). Solar radiation exerted the greatest effect, tending to depress activity.

During summer, solar radiation exerted a significant influence on activity, explaining 9% of the variance, and

again tended to depress activity. This effect was also evident in late summer.

Effect of Insect Harassment on Activity

At the beginning of June, biting and blood sucking insects became prevalent. The fly season reached a peak during the last half of June, then tapered off during July and August. The frequency distribution of insect harassment during two-week intervals from the beginning of May to the end of August is displayed in Fig. 3.4.

The predominant insect pests observed during June and July were mosquitoes (*Culicidae*), and horseflies and deer flies (*Tabanidae*). In late August, black flies (*Simulidae*) predominated.

During June and July, there was a definite daily rhythm in the level of insect harassment. Fig. 3.5 shows the number of observation intervals at each of five daily time periods in which high intensity harassment was recorded. A peak occurred in the early morning when mosquitoes were abundant. As temperatures rose in the morning mosquito harassment declined and biting flies increased in abundance. Between 11 a.m. and 4 p.m. the activity of horseflies and deer flies reached a peak. As conditions cooled in the evening mosquitoes again predominated. After nightfall there was little insect harassment.

Figure 3.4 Intensity of biting insect harassment between May and August. Sample size is indicated at the top of each column.

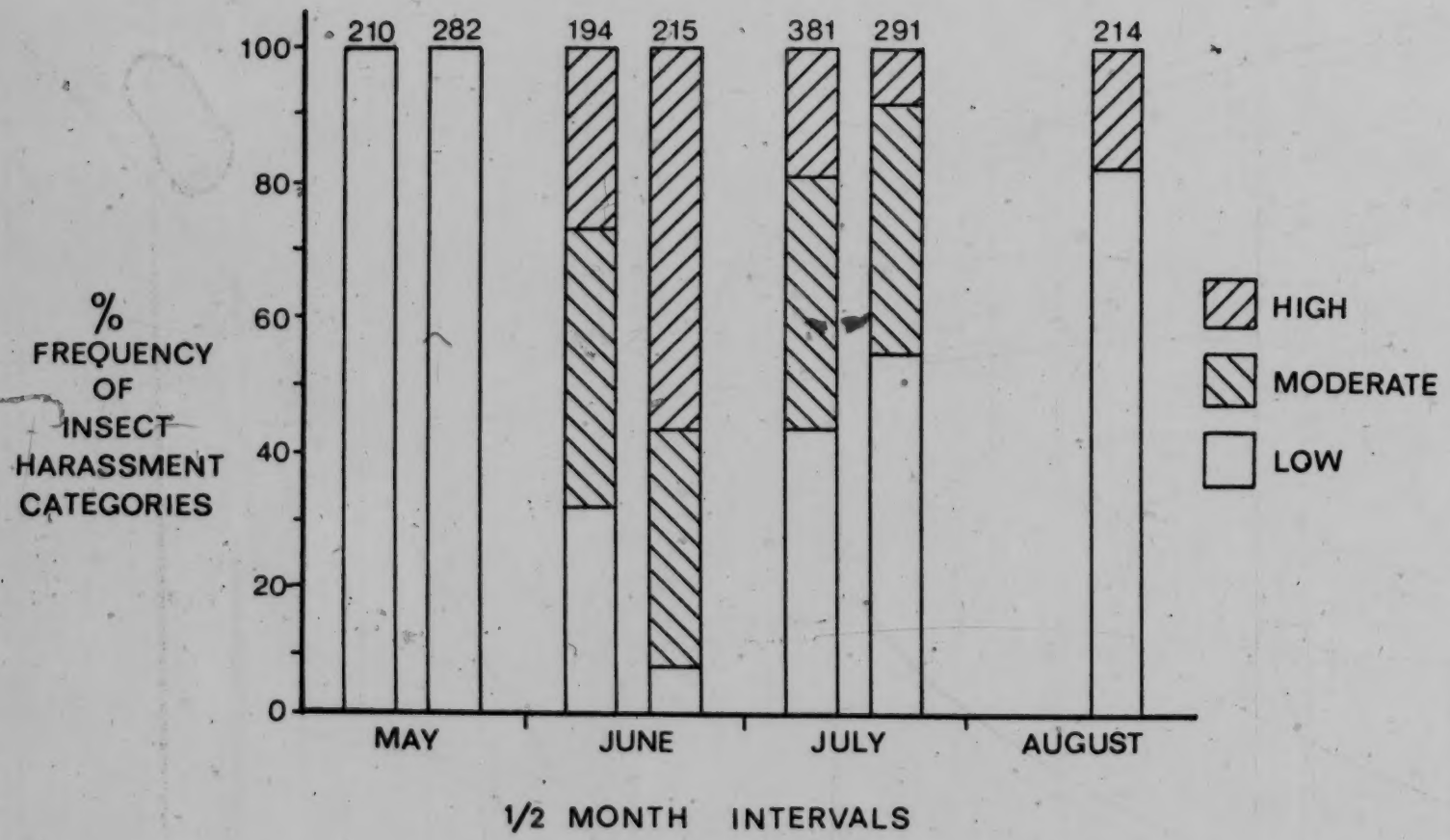
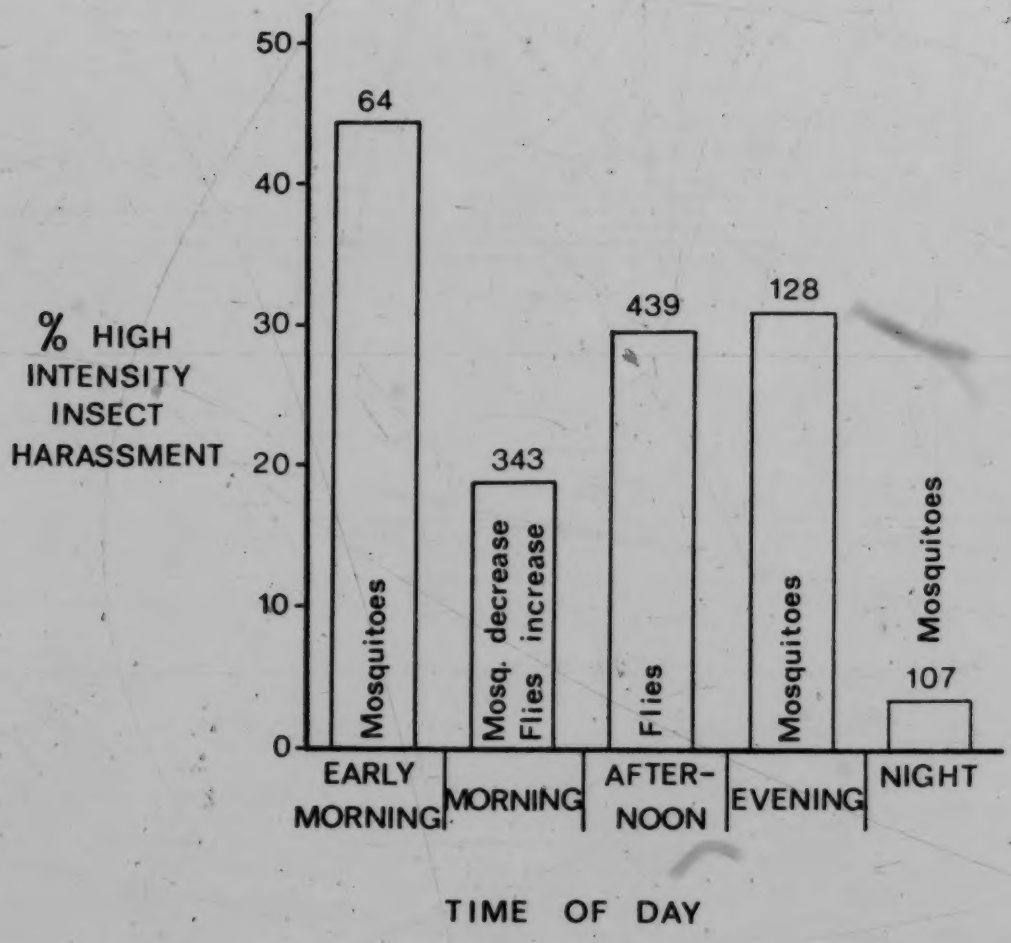

210
282
194
215
381
291
214
100
80
60
40
20
0
% FREQUENCY OF INSECT HARASSMENT CATEGORIES
HIGH
MODERATE
LOW
MAY
JUNE
JULY
AUGUST
1/2 MONTH INTERVALS

Figure 3.5 Daily pattern of intense insect harassment during June and July. Sample size is indicated at the top of each column.


% HIGH INTENSITY INSECT HARASSMENT
50
40
30
20
10
0
64
343
439
128
107
Mosquitoes
Mosq. decrease
Flies increase
Flies
Mosquitoes
Mosquitoes
EARLY MORNING
MORNING
AFTER-NOON
EVENING
NIGHT
TIME OF DAY

DISCUSSION

Circadian rhythms of wapiti were of two types. In late summer, fall, winter, and early spring a polyphasic pattern of alternating foraging and resting bouts occurred with approximately 4 or 5 cycles over a 24-hour period. The pattern was fundamentally different during spring and summer when foraging activity was biphasic with peaks occurring at sunrise and sunset. Similar activity patterns have been observed in other wild ruminants. Ozoga and Verme (1970) observed that the circadian rhythm of white-tailed deer in early winter consisted of 5 peaks of activity spaced 4 to 6 hours apart. Deer fed most heavily around sunrise, midday, sunset and twice during the night. With the exception of a period of aquatic feeding in late afternoon, the summer activities of moose were similar to the wapiti in this study, showing peaks in feeding at dawn and early morning and at sunset and the early part of the night (Belovsky 1978).

Both endogenous and environmental factors are involved in daily activity. Rhythmic short-term variations in nutritional requirements likely played an important role as an intrinsic determinant. The free-foraging ruminant is faced with the necessity of meeting nutrient requirements continuously so that regulation of food intake is an active ongoing process. McClymont (1967) recognized three general types of endogenous inhibitory stimuli to phagic behaviour; namely, energy-intake, distention and fatigue. Feedback

stimuli arise from the digestion and metabolism of nutrients. In ruminants, volatile fatty acids, end-products of rumen fermentation, appear to play a major role (Simkins *et al*. 1965). Distention stimuli arise from distention of the alimentary tract. In these herbivores the rate of passage of food from the rumen, which is a function of forage digestibility, governs the amount which can be consumed when the animal is eating to capacity (Baile and Forbes 1974).

The third category of regulatory stimuli results from the fatigue of prolonged foraging. Even when herbivores graze sparse, low quality forage so that a prolonged grazing time cannot compensate, feeding activity is not continuous. On sparse winter pasture wapiti in Yellowstone National Park were observed to undergo discrete bouts of foraging and yet malnutrition was responsible for heavy mortality (Craighead *et al*. 1973).

The basic rhythm of alternating foraging-resting bouts seen in the present study can be interpreted as repletion-depletion cycles. Particularly during the fall, winter and early spring when the diet had a higher fiber content, the observed activity cycles may have been the result of feeding to gut capacity then resting and ruminating until sufficient ingesta was cleared from the foregut allowing for further consumption.

When the wapiti were feeding on highly digestible forage in spring and summer, environmental factors modified

this cycle. The wapiti tended to feed in shorter bouts during the summer than at any other time and although feeding was restricted during the day it was engaged in frequently for short periods. This suggests that the summer rhythm may occur at a greater frequency than in other periods though this was not obvious because of the modifying influence of other environmental factors. von Berg (1978) noted that the frequency of feed-rest cycles in roe deer was greater in summer than during winter. The greater clearance rate of highly digestible summer forage may have permitted a greater number of activity cycles. On the other hand, the great abundance of highly digestible feed items may have permitted the wapiti to consume sufficient forage during the more environmentally favorable periods of the day; hence the biphasic pattern during spring and summer.

Other intrinsic physiological processes may be involved in determining activity cycles. The need to ruminate may motivate periodic rest periods. The rate of passage of food from the rumen and therefore the capacity of the animal to consume more food, is governed in part by the rate of microbial breakdown of ingesta and by the size of particles which can pass through the reticulo-omasal orifice. Rumination reduces particle size and enhances clearance of ingesta from the rumen.

Another physiological requisite of mammals is sleep or periods of rest. The requirement for and biological function of sleep remains enigmatic despite considerable research

(Ruckebusch 1975). In ruminants, resting periods are characterized by bouts of rumination and domestic species are known to experience three levels of awareness while ruminating; namely, alert wakefulness, drowsiness and slow wave sleep (Ruckebusch 1972). The reduced level of alertness usually seen in ruminating wapiti, may serve a reconstitutive purpose in addition to a digestive function. Morag (1967) suggested that in sheep deprived of rumination because they were fed finely ground food, sleep was essential as a replacement for rumination.

A number of environmental factors influenced the activities of wapiti. Primary among these was weather. The effects that weather had on activity, though frequently statistically significant, were never pronounced. Although weather can influence activity the animal has an option through habitat selection, to change micro-environmental exposure and yet continue in the same activity. Since the study area was highly heterogeneous it is likely that the animals were able to moderate meteorlogical extremes without necessarily alterating their activity.

Ambient temperature, wind velocity and solar radiation are major components of the thermal environment. Responses to the thermal environment depend on attributes of the animal such as size, subcutaneous fat, nutritional status and external insulation.

When in winter pelage, wapiti in this study generally responded to increasing heat loads by decreasing activity.

Although this response was noted as solar radiation increased when the wapiti were in summer coat, the response to ambient temperature as a single factor was less clear. Mobile activities occurred with similar frequency over a wide range of temperatures and deviated only at extremes of heat and cold.

While the increase in activity at very high temperatures in summer coat may have been a response to harassment by biting insects, the same response to very cold temperatures in summer and the trend in winter coat towards increasing activity in cold environments probably reflected attempts to maintain thermal balance. Increases in activity largely represented increased foraging. This trend in relation to increasing heat has been correlated with decreases in foraging activity and/or feed intake in cattle (Hafez *et al* . 1969), the African buffalo (Grimsdell and Field 1976), and moose (Belovsky and Jordan 1978).

In hot environments, reduced feeding benefits the animal in two ways. It permits the opportunity to seek a cooler resting microenvironment and as a result of a reduced level of feed intake the heat increment of feeding (a thermal loading factor) is reduced. In cold environments increased feeding activity can be interpreted as an attempt to offset higher thermoregulatory costs. The ability of the grazing animal to compensate by increasing food intake depends on a number of factors. The availability and quality of forage and the cost of acquiring it are obviously

important in energy balance.

The nutritional condition of the animal is another factor. Ozoga and Verme (1970) found that as deer lost condition feeding activity was restricted increasingly to the warmer parts of the day. Moen (1968) suggested that shelter seeking by deer in cold weather may or may not occur depending on nutritional status and also suggested that when the diet was sufficient to maintain a positive energy balance, the animals may elect not to seek shelter even under highly unfavorable conditions. Reductions in activity in the cold has been noted in domestic cattle. Malachek and Smith (1976) observed that herefords spent more time grazing on warm days than on cold days in winter when temperatures ranged between -24 and 5°C. A number of workers have noted reduced activity of white-tailed deer in the cold (Silver and Colvos 1957, Banasiak 1961, Day 1963).

Being active in the cold results in a greater heat loss than when an animal is lying down (Gates and Hudson 1979). Under conditions of forage scarcity and poor quality it could be energetically more favorable to rest and seek shelter rather than to forage under extremely cold conditions. The reduced activity of wapiti in Yellowstone Park in winter (Craighead *et al*. 1973) is probably an example of such a decision although low availability of feed in that study may have been a factor.

Reduced activity in the cold was not obvious in the present study, suggesting that thermal and nutritional

conditions were never critical. Murie (1951) also noted the hardiness of wapiti stating that 'extreme cold apparently does not greatly affect them'. However, Gaffney (1941) observed that wapiti reduced their activity when ambient temperature fell to -43°C. Although the lower threshold for eliciting a reduction in activity was not seen in this study, there probably is a point where it would occur if the ambient temperature fell to a sufficiently low level.

The thermal environment played a role in determining circadian activity patterns of wapiti. They tended to rest in the afternoon in mid winter in fully exposed sites, apparently capitalizing on solar radiation which was highest at this time of day. Loveless (1964) reported that mule deer also sought direct sunlight on cold days.

During the spring and summer, foraging was most prevalent in the morning and evening. This pattern avoids activity in the warmest parts of the day, a tendency which has been commonly reported for other species. Night activities generally tended to be evenly divided between resting and foraging with the exception of spring and summer. During summer the wapiti fed for a greater proportion of the night than at any other season. The tendency to increase night grazing under hot environmental conditions is commonly noted in cattle (Hafez *et al* . 1969). Craighead *et al* . (1973) also noted increased foraging by wapiti during the night in summer compared to winter.

It is more difficult to explain the large increase in

bedding during nocturnal hours in the spring. Compared to about 50% in other seasons, 74% of the night was spent resting. Since the nights were still cool during the spring yet the wapiti had lost or were losing their winter pelage and hence external insulation was reduced, nighttime resting could have been an energy conserving tactic.

The pronounced tendency to feed in the early morning in the majority of seasons is in agreement with observations on other domestic and wild herbivores. A rapid change in environmental lighting has been proposed as an important time indicator causing the initiation of feeding at dawn in cattle (Hafez *et al*. 1969), impala (Jarman and Jarman 1973), Thomson's gazelle (Walther 1973) and domestic sheep (Arnold and Dudzinski 1978), and appears to play a similar role in wapiti.

Insects seemed at times to cause severe distress to the wapiti. The increase in mobile activities at high ambient temperatures in the summer may have been due to agitation by horseflies since their activity reached a peak at high ambient temperatures. Blickle (1959) demonstrated that temperature was the main factor affecting swarming of horseflies. Adult flies were not active at air temeratures below 13°C and maximum swarming occurred at temperatures above 25°C. Much of the mobile activity engaged in by the wapiti during the afternoon on hot summer days was initiated by biting fly disturbance. Altmann (1952) reported similar responses of wapiti to severe fly disturbance.

In Thomson's gazelle (Walther 1973) and impala (Jarman and Jarman 1973), the activities of herd members are coordinated to a degree which varies with different types of activities and between different times of the day and year. Lewis (1977) working with eland (*Taurotragus oryx*), onyx (*Oryx gazella*), buffalo and cattle, noted that the distribution of activities for individuals of the same species during the same day showed similar patterns. In the present study, coordination ranged between 84% and 91% throughout the year.

Walther (1973) suggested that three factors were involved in determining coordination. The first was that individual animals within a group are theoretically exposed to the same environmental stimuli and physiological rhythms. Hence entrainment of the biological clock should be similar for all herd members. An example of such an effect is the apparent influence of sunrise on wapiti; throughout most of the annual cycle the herd responded to the Zeit Gerber by commencing to feed.

Activities of individuals can influence those of others through contagion or social facilitation (Tinbergen 1951). McCullough (1971) enumerated the stimuli generated as a result of activity which could be involved in coordinating group behaviour in wapiti. Visual communication plays an important role since every act conveys information to other herd members in view. A range of auditory signals are generated in the course of various activities. McCullough

(*op cit.*) described several involuntary sounds such as grinding of teeth, snapping of twigs, footsteps and creeking joints, stomach grumbling and eructation in resting wapiti. Olfaction is highly developed in wapiti and likely plays a role in coordinating activity by enabling an individual to determine if a noise generated by an unseen animal is caused by a conspecific.

In general, the herd member continuously receives sensory input generated involuntarily from other group members. However, active or voluntary signals also play a role in coordinating activity. The most obvious example is the harem tending behaviour of mature bulls during the rut. Dominant bulls attempt to keep group members together (Struhsaker 1967) resulting in a large degree of coordination of the activities of harem members. Coordination is also reinforced by individuals actively approaching other group members and inducing them to alter their activity.

A large number of endogenous factors and features of the natural environment act simultaneously to determine the activity of wapiti. In addition to these, the activities of other species can affect behaviour and more specifically activity patterns. Predators and man are the two animals to disturb the basic daily pattern of grazing wild herbivores. Since neither predators nor human disturbance were relevant in this study the observed behavioural patterns represent basic unaltered responses to endogenous and environmental

stimuli and provide a useful background against which the behaviour of disturbed populations can be compared.

Chapter 4

HABITAT SELECTION

INTRODUCTION

Animals tend to be restricted by physiological or behavioural responses to physical and biotic features of their environment. The result is that different species exhibit different patterns of occupation. These are manifested in spatial, temporal, and functional variations in patterns of habitat use.

For many animals habitat selection is an active process which requires them to make decisions on what is acceptable or preferable in terms of environmental attributes. Heredity plays a role in determining innate habitat preferences by fixing behavioural predispositions to environmental cues (Wecker 1964). Learning plays a dominant role, particularly in higher vertebrates and can occur at a very early age. For example, neonatal pronghorn antelope fawns appear to seek seclusion in cover resembling that in which they were born (Autenrieth and Fitcher 1975). Socially-facilitated learning of habitat selection is expressed in traditional patterns of use, a phenomenon which is particularly evident in bighorn sheep (*Ovis canadensis*) (Geist 1971a). Tradition-formation is presumably based on the attractiveness of the rest of the herd with crystallization of search images arising from familiarity with certain areas. Learning also arises from mimicry of the behaviour of other animals (Edwards 1976).

Learning by association with proximate environmental stimuli is of major significance in the development of habitat preferences. The polarity of the stimulus depends to a large degree on the innate behavioural and morphological predisposition of the animal and to the nature of the stimulus. Physical barriers and terrain factors can be strong determinants of use in domestic animals on pasture (Arnold and Dudzinski 1978).

In northern environments, snow cover is a particularly influential factor for wild herbivores (Kelsall and Prescott 1971). Species-characteristics largely determine ability to handle snow cover. Chest height, foot loading, and preferred vertical feeding stratum are important anatomical and behavioural features. The tolerance of a species to climatic factors is also a function of physical and physiological attributes such as body size, insulation, and level of acclimitization.

Habitat selection is determined to a marked degree by the distribution, availability, and quality of resources. Distances to water, salt, and cover are important and for the grazing animal, forage factors exert a strong influence on occupational patterns (Arnold 1964, Bell 1971, Ferrar and Walker 1974, Jarman 1974).

The wapiti is a highly evolved Old World deer which arrived on the North American continent during the Pleistocene, probably more recently than the interglacial preceding the Wisconsin glaciations (Guthrie 1966). Similar

to the European red deer, the wapiti is an ecotone species which is highly opportunistic. This is manifested in its catholic food habits (Kufeld 1973), wide geographic range (Murie 1951), and ability to migrate to more favorable areas within its home range (Knight 1970). Wapiti tend to occupy more open country than red deer.

Larger body size in wapiti is a result of selection under conditions of geographic dispersal and colonization of an unoccupied and highly favorable environment during post glacial times (Geist 1971b). Large body size permits an ungulate to tolerate wider extremes in environmental exposure and to consume more fibrous, less digestible forage (Bell 1971). Consequently, it is expected that wapiti should consume a lower quality diet and be less responsive to cold weather than, for example, the smaller white-tailed deer. This would be reflected in a reduced need for cover and selection of feeding sites should be less influenced by thermal factors than by forage factors. Being an opportunist and generalist, it can be expected that the wapiti will exhibit flexibility in habitat use, versatility in foraging patterns, and be responsive to microenvironmental variations in snow conditions, forage quality and abundance, and will seek shelter more frequently when heat stress is potentially high.

The present study attempted to examine habitat use of wapiti in relation to a number of environmental factors.

METHODS

Habitat Use

An aerial photograph was used to plot movements of the herd; a grid (15 x 15 m) was used to record location coordinates of the herd every 10 minutes. Each coordinate was subjectively described according to cover type. The central position of the largest group performing a common activity was the basic data unit. The positions of herd members not engaged in the dominant activity were ignored.

Plant Phenology and Seasons

Records were maintained on phenological development of the dominant grass species (bluegrass and brome) and for woody plants. This served to identify seven major time periods (Table 4.1). Winter subperiods were based on snow conditions.

Meteorological Conditions

Measurements were taken every 10 minutes of ambient temperature, solar radiation and wind at the nearest exposed site to the group's location. If the animals were sheltered, a measurement of solar radiation also was obtained by averaging individual values for each wapiti taken above their backs. The reduction in wind velocity also was estimated. Solar radiation ($ly.min^{-1}$) was measured with a hand-held radiometer (Jochem 1976). Wind velocity was subjectively rated on a scale of 0 to 5. These categories were later assigned values of 0, 0.9, 2.7, 5.4, 8.9 and 13.4 m/sec respectively. Notes were kept on precipitation. Snow

Table 4.1 Phenological stages during the annual cycle.

Stage	Inclusive Dates (1977-78)	Description
Mature-Leaves abcised	Sept 21-Nov 21	Grasses maturing and curing, leaves on woody species largely abcised.
Dormancy	Nov 22-Feb 15	Grasses cured, snow on ground.
Weathered	Feb 16-Apr 21	Grasses exposed but leached by snow melt, rain and sun.
First Growth	Apr 22-May 7	Initial period of grass growth; grasses very short, less than 5 cm.
Vegetative Growth	May 8-June 15	Rapid growth of grasses, leaf development and flush on woody plants.
Flower Development	June 16-July 30	Reproductive phase of grass phenology; forbs abundant.
Mature-Leaves present	Aug 1-Sept 20	Post seed set in grasses; forbs declining in abundance; still green on woody plants.

depth was measured with a meter rule and notes were kept on crusting and melting throughout the study area.

Insect Harassment

Notes were kept on the intensity of harassment to the wapiti by biting and blood-sucking insects. Harassment was recorded in five categories from nil to severe.

Statistical Methods

Use of vegetation types in relation to plant phenology, snow cover, rain and insect harassment was analysed by contingency table analysis using G-test (Sokal and Rohlf 1969), Chi square test (Nie *et al* . 1975), or by testing differences between two proportions (%) with a t-test (Sokal and Rohlf 1969).

Seasonal shelter seeking behaviour of wapiti in response to meteorological factors (wind, temperature, solar radiation) was analysed using step-wise multiple regression (Nie *et al* . 1975).

RESULTS

Cumulative Use of Vegetation Types for Foraging

The frequency distribution of habitat occupancy for foraging for all cases is presented in Table 4.2. If habitat selection was random the expected distribution of use would be proportional to the relative abundance of habitat. As indicated by the overall G statistic and category-specific t-statistics, habitat occupancy deviated significantly overall, and within each vegetation type, from the aerial

Table 4.2 Cumulative habitat use for foraging.

Cover type	Observed %	Observed N	Expected %	Expected N	t (t at .001=3.29)	Ratio O/E
Forest Upland	30.1	505	47.4	796	10.35	-0.64
Meadow Lowland	49.6	833	19.1	321	19.10	2.60
Meadow	8.6	144	4.4	74	5.00	1.95
Willow	6.3	106	11.9	200	5.71	-0.53
Sedge Wetland	4.4	74	11.5	193	7.80	-0.38
Open Water	1.0	17	5.7	95	8.16	-0.18
Total	100.0	1679	100.0	1679		
G=77.416	$x^2(.01,5)=15.086$.					

coverage of the habitat types. A measure of this deviation, a habitat selection index, was obtained by determining the ratio between observed and expected frequencies of use, then assigning a positive or negative sign to denote whether use was greater than or less than expected.

Although poplar forest covered 47.7% of the area its overall use for foraging was only 30.1%, yielding a selection index of -0.64. Similarly willow stands and sedge wetlands were used considerably less than expected from a random distribution of use. The distinct preference of wapiti for feeding in meadows is indicated by the high preference coefficients for the upland and lowland meadow types. Use of open water for foraging was incidentally associated with feeding at the edge of ponds and sedge wetlands.

Influence of Phenological Succession

Occupational patterns and foraging tactics responded to changes in the forage resource and were a function of the seasonal progression of plant phenology in each community (Fig.4.1,Table 4.3).

The initiation of the growing season for grasses and sedge occurred about April 22. During the 'first growth' period new growth grasses were evident though not dominant relative to weathered vegetation. Grass leaf lengths ranged up to 5 cm.

Figure 4.1 Habitat occupancy for foraging in relation to plant phenology.

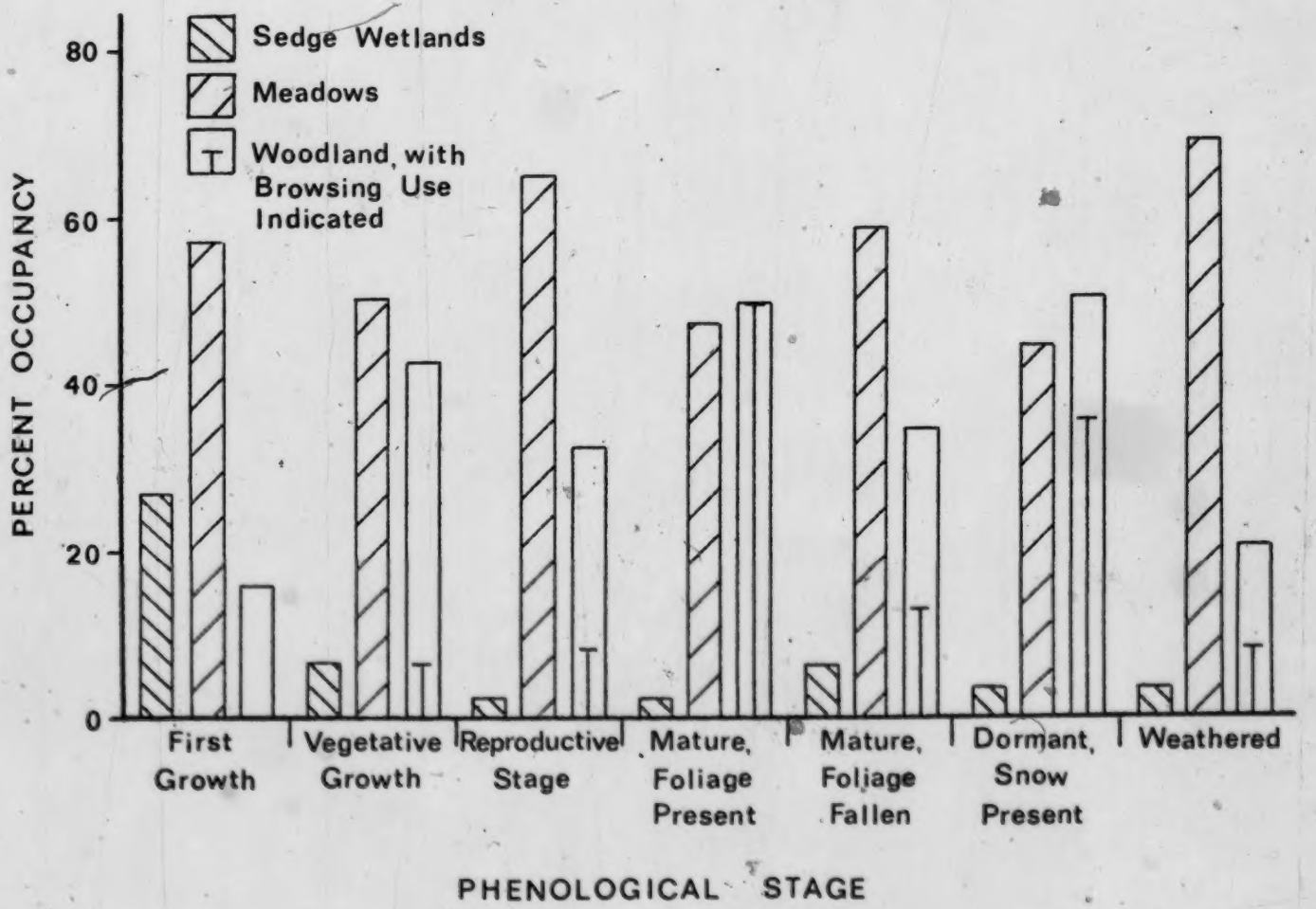

Sedge Wetlands
Meadows
Woodland, with Browsing Use Indicated
PERCENT OCCUPANCY
80
60
40
20
0
First Growth
Vegetative Growth
Reproductive Stage
Mature, Foliage Present
Mature, Foliage Fallen
Dormant, Snow Present
Weathered
PHENOLOGICAL STAGE

Table 4.3 Habitat use (%) for foraging of cover types in relation to plant phenology.

Phenological Stage	Cover Type: Sedge Wetland	Upland Meadow	Lowland Meadow	Willow Stands	Poplar Forest	Sample Size
First Growth	26.7	57.3	0.0	10.7	5.3	75
Vegetative Growth	6.7	41.0	9.3	4.5	38.5	268
Reproductive Stage	2.3	55.0	10.1	8.5	24.0	258
Mature leaves present	2.3	27.9	19.8	3.5	46.5	86
Mature, leaves fallen, no snow	6.1	49.7	9.5	9.6	25.1	342
Dormant snow, cover	3.7	34.7	10.2	6.8	44.6	523
Weathered	3.9	66.9	7.9	0.0	21.3	127

Another cover type which offered significant quantities of green vegetation during the first growth stage was sedge wetlands. Here sedge shoots and even submerged green aquatic vegetation were consumed by the wapiti.

The wapiti also foraged to a lesser extent in willow stands and poplar forests. Browse plants were in the leaf bud enlargement stage. However, the wapiti fed very little on browse, preferring to graze in the woodland cover types. The proximity of willow stands to sedge meadows and indeed the considerable overlap of species composition in the field layer between these two cover types explains part of the use received by willow stands. Some grasses shoots were evident in the poplar forests and it was mostly this material which was consumed by the wapiti.

By May 9, the wapiti's diet consisted largely of grass shoots. During the ensuing month grasses underwent a phase of rapid growth. This phenological stage was referred to as the 'Vegetative Growth' period. Foraging emphasized consumption of grasses in meadows and poplar forest. Browsing occurred to a limited extent in wooded areas, occupying 6.3% of the feeding budget. When browsing; the wapiti consumed foliage which underwent leaf expansion and leaf flush during mid May.

From mid June to the end of July, grasses underwent the 'Reproductive' phase of their annual phenological cycle. Forbs achieved their maximum status in the various plant communities during this period. Foraging sites were

primarily located in the meadows and use of woodlands declined slightly. Browsing in the latter types remained at a low level (8.2%). In both meadows and woodlands, wapiti appeared to prefer forbs over other forages.

By the latter part of August, grasses began to cure and forbs declined in abundance. This phenological stage was termed 'Mature, browse foliage present', referring to maturation of grasses and separating it from the period after leaf abcission. During late August the wapiti responded to the phenological changes in the field layer by shifting foraging emphasis towards browse foliage (hazelnut and aspen). Occupancy of woodland types increased and all of this was directed to browsing. Both leaves and terminal portions of twigs were consumed.

Accompanying leaf abcission from the deciduous browse species in late September, grasses matured further and forbs declined in abundance with each successive frost. During the fall the wapiti shifted back to foraging in the field layer of meadows though still foraging to a considerable extent in woodland cover types. Browse consumption in the latter communities stressed consumption of foliage lingering on shrubs. This tactic was a minor component of the foraging effort (13.5%). Grazing in the woodlands was directed towards consumption of green vegetation, both grasses and forbs which were still green (e.g. *Cornus canadensis*) or those which had withered yet remained standing (e.g. *Urtica spp.*).

During the 'Dormant, snow present' stage referring to the winter months (December to late March), snow cover was a major determinant of occupational patterns for foraging.

Influence of Snow on Selection of Foraging Habitat

Permanent snow cover arrived at the end of November. It remained shallow (<20 cm) until the end of December when a number of successive heavy snow falls resulted in accumulations of between 35 and 45 cm. The snow cover remained deep and light during January and the first half of February. There was no apparent variation in snow characteristics between the different vegetation types.

During the last third of February, warm windy weather conditions effected rapid changes in the snow cover. Snow depths were reduced from greater than 35 cm to 10 cm or less in more exposed sites and in the forest depths were reduced to 20 to 25 cm within a few days. Patches of upland meadow were exposed on knolls and on a south facing slope. By mid March much of the grassland was free from snow cover though some remained in the forest.

The wapiti altered habitat selection patterns and foraging tactics in response to the changing snow regimes as shown in Table 4.4. Under shallow snow conditions the frequency of use of wooded cover types for foraging increased from the fall. Although this was not significant statistically ($P > .05$) as determined by a t-test, it indicated a change in foraging habits. The marked increase ($P < .001$) in browsing frequency from fall (13.5%) to the

Table 4.4. Habitat use (%) for foraging in relation to snow conditions.

Snow Conditions	Cover Type: Sedge Wetland	Upland Meadow	Lowland Meadow	Willow Stands	Poplar Forest	Percent Browsing	Sample Size
No snow (Fall)	6.1	49.7	9.4	9.6	25.1	13.5	342
Shallow (<20 cm)	4.8	34.8	18.3	1.2	40.9	28.7	164
Deep (35-45 cm)	2.5	35.2	1.9	12.3	48.1	60.4	162
Snow-free patches in meadows	3.6	73.5	1.0	3.1	18.9	22.0	196
Meadows snow-free, reduced depth in trees	3.9	66.9	7.9	0.0	21.3	8.7	127

shallow snow period (28.7%) supports this interpretation.

Shallow snow (< 20 cm) appeared to have little effect on forage selection during grazing. Pawing was used to initiate crater formation but more commonly snow was simply pushed aside with the muzzle. Again the wapiti appeared to select green plant parts in preference to cured material. In the forest, dried browse foliage which remained on branches was consumed whenever encountered.

With the arrival of deep snow in late December and early January more emphasis was directed to feeding in woodland cover types. Cratering during grazing was not observed in woodlands; all use of these types was for browsing. Willow stands received increased use in this period. In the deep snow cover grazing in meadows was effected by preparing craters. This was done by alternate pawing with the front legs using long strokes to toss snow to the side and rear. Because the snow was light the walls of the crater often fell back into the crater covering the herbage. When cratering in deep snow the wapiti appeared to do little sampling, tending instead to construct continuous craters up to 5 meters long. The harvest of forage from the craters was particularly non-selective with virtually all plant material being consumed.

At the end of February and beginning of March, the wapiti responded to warmer conditions and exposure of patches of meadow by heavily shifting emphasis towards relatively non-selective grazing in these sites. Circadian

fluctuations in ambient temperature and solar radiation resulted in changes in snow hardness which affected the effort required for feeding. The snow was dense and granular in texture. During the day when ambient temperature was above freezing and solar radiation warmed the snow it was soft and easily moved aside with the muzzle. When temperatures were below freezing, e.g. at night, the snow became extremely hard making exposure difficult. Depending on snow hardness the wapiti employed two types of pawing strokes. For the soft granular shallow type they used a slow sweeping long stroke similar to that used for deep light snow conditions. For hard, densely packed snow they used a rapid chopping motion.

At the end of March, snow cover had largely melted in both the meadows and woodlands. Most of the foraging effort was concentrated in the meadows with little in the wooded areas of which less than half was browsing. Once again the wapiti appeared to exhibit some selectivity while grazing and were observed to select for green plant material.

Influence of Weather

The influence of the three weather variables, ambient temperature, solar radiation and wind, on habitat selection by wapiti (Table 4.5) differed for resting and feeding in each season (Tables 4.6,4.7). In each case the amount of variance explained by these models was higher for resting.

The strongest influence of weather variables was on resting habitat selection in mid winter (R^2 = .779). Wind

Table 4.5. General habitat selection in response to weather. Results of a multiple stepwise regression analysis.

Season	Statistic	Ambient Temperature (°C)	Solar Radiation (W/m²)	Wind Velocity (m/sec)	Multiple R^2
Fall	B	0.007	0.005	0.065	
	R^2 change	0.026***	0.102***	0.016***	0.144***
Early Winter	B	-0.006	0.010	-0.022	
	R^2 change	0.033***	0.001	0.005	0.038**
Mid Winter	B	-0.020	-0.003	0.036	
	R^2 change	0.202***	0.011**	0.019**	0.232***
Late Winter	B	0.010	0.002	-0.016	
	R^2 change	0.016*	0.008	0.012**	0.036**
Early Spring	B	-0.022	0.003	-0.011	
	R^2 change	0.027**	0.032***	0.009*	0.068***
Spring	B	-0.004	0.000	0.053	
	R^2 change	0.002	0.000	0.015**	0.017**
Summer	B	0.004	-0.005	-0.002	
	R^2 change	0.002***	0.086***	0.000	0.088***
Late Summer	B	0.021	0.010	0.385	
	R^2 change	0.038***	0.172***	0.014**	0.224***

* P<.05 ** P<.01 *** P<.001

Table 4.6. Cover selection during bedding in relation to weather. Results of a multiple stepwise regression analysis.

Season	Statistic	Ambient Temperature (°C)	Solar Radiation (W/m²)	Wind Velocity (m/sec)	Multiple R^2
Fall	B	0.011	0.008	0.062	
	R^2 change	0.022**	0.280***	0.015*	0.317***
Early Winter	B	-0.016	0.004	-0.044	
	R^2 change	0.253***	0.008	0.019	0.280***
Mid Winter	B	-0.025	-0.002	0.108	
	R^2 change	0.178***	0.006	0.596***	0.779***
Late Winter	B	-0.014	0.010	-0.012	
	R^2 change	0.013	0.164***	0.008	0.185***
Early Spring	B	-0.027	-0.001	-0.043	
	R^2 change	0.086***	0.001	0.074***	0.161***
Spring	B	0.001	0.002	0.063	
	R^2 change	0.001	0.009	0.042***	0.052***
Summer	B	-0.005	-0.006	-0.003	
	R^2 change	0.002	0.128***	0.000	0.130***
Late Summer	B	0.035	0.012	0.311	
	R^2 change	0.011***	0.263***	0.014	0.387***

* P<.05 ** P<.01 *** P<.001

Table 4.7. Cover selection during feeding in relation to weather. Results of a multiple stepwise regression analysis.

Season	Statistic	Ambient Temperature (°C)	Solar Radiation (W/m^2)	Wind Velocity (m/sec)	Multiple R^2
Fall	B	0.005	0.032	0.055	
	R^2 change	0.011*	0.052***	0.019**	0.082***
Early Winter	B	0.008	0.008	-0.012	
	R^2 change	0.010	0.000	0.002	0.012
Mid Winter	B	-0.006	-0.002	-0.006	
	R^2 change	0.006	0.003	0.001	0.010
Late Winter	B	0.016	-0.003	-0.021	
	R^2 change	0.021*	0.014	0.064***	0.099***
Early Spring	B	-0.022	0.003	-0.002	
	R^2 change	0.044**	0.022*	0.000	0.066**
Spring	B	-0.011	-0.003	0.026	
	R^2 change	0.014*	0.017*	0.003	0.033*
Summer	B	0.014	-0.002	0.015	
	R^2 change	0.019*	0.011***	0.000	0.031*
Late Summer	B	-0.002	0.008	0.000	
	R^2 change	0.000	0.09*	0.000	0.079*

* P<.05 ** P<.01 *** P<.001

appeared to exert the greatest influence (individual R^2 = .596) but ambient temperature also was important (R^2 .178). Wapiti sought cover for resting as the temperature declined and winds increased. Solar radiation did not have a significant effect on resting habitat selection in mid winter although wapiti were occasionally observed to select bedding sites in the meadows in the bright afternoon sun.

In late summer, fall and late winter wapiti sought cover as solar radiation increased. During the summer this trend was reversed. In each of these seasons solar radiation accounted for the majority of explained variance. The unexpected trend to seek exposure to sun in the summer, may be explained by the observation that as the thermophilic biting insects increased activity, the wapiti bedded closer to the area of treated posts which offered little shade.

Sheltering Behaviour

Wapiti have the option of seeking amelioration of uncomfortable thermal conditions not only by seeking different habitats but also by seeking sites in one habitat in which the microclimate is a function of the sheltering effect of an adjacent type. For example, wapiti may elect to rest in a meadow in the shade generated by an adjacent stand of trees. This behaviour was investigated in the following manner. At each observation interval data were collected for solar radiation in the open and at the site of the predominant herd activity. This permitted an evaluation of shade selection in relation to weather. Multiple stepwise

regressions were performed in which selection of shade (treated as a dichotomy) was the dependent variable and teperature, solar radiation and wind were the independent variables. Seasons which were similar in weather conditions were grouped. Since weather influences resting site selection to a greater degree than foraging only cases in which the predominant herd activity was resting were included in this analysis. The results are presented in Table 8. For illustration, a cross tabulation of occurrence in the shade in relation to categories of solar radiation was generated. The r value in each graph is the single bivariate correlation coefficient generated from the MSR analysis.

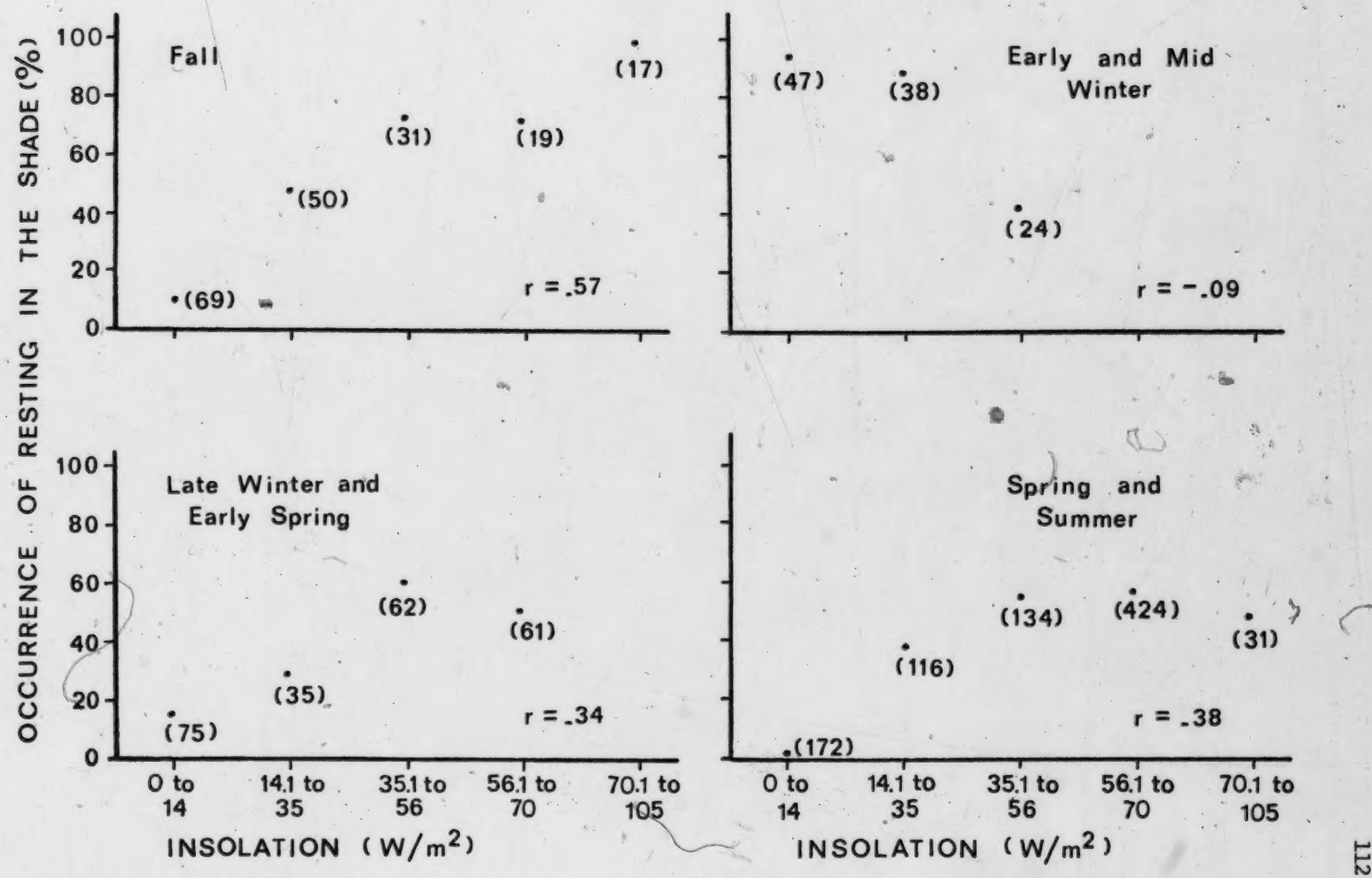
Shade selection in the fall was a function of the intensity of incident solar radition. The other two factors exerted little influence. The strong bivariate correlation between shade seeking and solar radiation is visually apparent in Fig. 4.2 for the fall. In both the early to mid winter, and late winter to early spring periods, ambient temperature was the major factor determining shade-seeking while resting. During early and mid winter, shaded sites were avoided more as temperature increased. This reflected the generally colder temperatures encountered during that time. In late winter to early spring, increasing temperatures again resulted in shade seeking. Occurrence in the shade in spring and summer was moderately explained by increasing solar radiation (R^2 = .185) and was positively

Table 4.8. Occurrence of wapiti in shade while bedding in relation to weather. Results of a multiple stepwise regression analysis.

Season	Statistic	Ambient Temperature (°C)	Solar Radiation (W/m^2)	Wind Velocity (m/sec)	Multiple R^2
Fall	B	0.004	0.675	0.023	
	R^2 change	0.003	0.322***	0.000	0.326***
Early & Mid Winter	B	-0.039	-0.336	0.018	
	R^2 change	0.493***	0.055***	0.001	0.549***
Late Winter & Early Spring	B	0.044	0.123	-0.046	
	R^2 change	0.263***	0.005	0.021***	0.289***
Spring & Summer	B	-0.015	0.659	-0.096	
	R^2 change	0.021	0.146***	0.018	0.185***

*** P<.001

Figure 4.2 Occurrence of resting wapiti in shade in relation to solar radiation at different times of the year.


OCCURRENCE OF RESTING IN THE SHADE (%)
Fall
(69)
(50)
(31)
(19)
(17)
r = .57
Early and Mid Winter
(47)
(38)
(24)
r = −.09
Late Winter and Early Spring
(75)
(35)
(62)
(61)
r = .34
Spring and Summer
(172)
(116)
(134)
(424)
(31)
r = .38
0 to 14
14.1 to 35
35.1 to 56
56.1 to 70
70.1 to 105
INSOLATION (W/m²)

related to this variable contrary to what was indicated in Table 8. This difference can be explained on the basis of microhabitat selection for shade within open habitat types. Although temperatures ranged widely from 2 to 27°C and averaged 11.5 and 15.2°C for spring and summer respectively this variable affected shade selection very little.

Influence of Insect Harassment

Harassment by insects (*Culicidae* and *Tabanidae*) began at the end of May. The degree of annoyance inflicted by these insects varied from negligible in early May to high at the end of June and beginning of July.

Habitat selection during foraging periods was apparently little affected by the intensity of fly harassment (Table 4.9). However during resting periods there were some distinct shifts in habitat occupancy. The most evident alteration was use of the area around and between the treated posts. In constrast to periods without fly harassment, areas near the treated posts were used heavily (40-50%) whenever biting flies were active.

The other shift in habitat use for resting occurred at high levels of biting fly activity in wetland areas. Wapiti frequently were observed standing in water up to their flanks in order to protect their legs from attack by flies.

Table 4.9. Habitat use (%) for foraging and resting in relation to insect harassment.

Level of Insect Harass-ment	Foraging				Resting				
	Wetland	Meadows	Woodland	N	Wetland	Meadows	Woodland	Treated Posts	N
None	6.7	48.4	44.9	315	4.5	66.6	29.0	0.0	311
Very low	0.0	70.5	29.2	119	0.0	43.7	16.0	40.3	288
Low	1.7	44.1	54.3	59	0.6	26.5	22.2	50.0	162
Moderate	0.0	72.5	27.5	69	0.0	39.1	14.1	46.8	156
High	7.4	58.0	34.5	81	16.1	17.7	20.8	45.1	193

DISCUSSION

Selection of cover types by wapiti while resting or feeding was influenced by a number of biotic and physical environment factors. The factors which influence feeding habitat selection appeared to be largely forage factors. Weather influenced site selection only slightly. Acquistion of food energy and nutrients was probably the primary motivation.

The lack of responsiveness of foraging wapiti and red deer to weather conditions has been noted by other workers (Murie 1951, Staines 1976). There are a number of factors which may uncouple a grazing ungulate from its thermal environment. First, it may elect to forage only during more favorable periods of the day. The tolerance of an animal to climatic extremes also is a function of its nutritional status, size, and thermal insulation. Nutritional status affects thermal tolerances by determining the ability of an animal to increase heat production without serious depletion of tissue energy reserves. The heat increment of feeding (Webster 1972) is an important source of heat in cold environments. Body size influences thermal balance in relation to the ratio of surface area to mass. Larger animals are more resistant to heat loss by virtue of this relationship; hence, it is expected that wapiti should be less responsive to cold weather than smaller deer.

In northern environments, thermal insulation of the pelage of ungulates varies seasonally (Moote 1955, Ryder

1977). Internal insulation also varies seasonally with deposition and catabolism of subcutaneous fat depots. On the basis of these factors, it is expected that during the fall when wapiti are fat, on a good nutritonal plane and in winter coat, they should be most sensitive to heat stress. Accordingly, selection of shaded sites for feeding and bedding was most obvious in late summer and fall. In contrast, during the late winter period when wapiti are in poor condition and forage availability and quality are low, wapiti should be most sensitive to cold stress. Unfortunately, due to mild weather encountered during this period of the year this hypothesis was not tested.

Wapiti were most responsive to the meteorological environment when selecting bedding sites. While solar radiation exerted a maximum effect in late summer and fall when ambient temperature was high, wind was the major factor determining shelter seeking during January and February, the coldest period of the study. Hence heat stress was avoided by shelter-seeking in the fall and cold stress was avoided in the mid winter period by the same tactic. This indicates the complexity of the interactions between all components of the thermal environment and is further complicated by the animal's ability to respond thermogenically, a function of degree of acclimatization and nutritional status.

Beall (1976) demonstrated the role of solar radiation and temperature in selection of bedding sites by wapiti during the winter. During the day selection for exposure or

shaded sites depended on temperature. When temperature ranged between -18 and -12°C wapiti selected less shaded sites than when between -4 and 2°C. The important role of shelter in absence of solar radiation was demonstrated when wapiti bedded on open slopes during the day but in dense timber at night (Beall *op cit.*).

During spring and summer the wapiti were only slightly responsive to meteorological conditions. They appeared to respond to increasing solar radiation in the summer by seeking exposed sites where thermal stress was assured. This apparent contradiction was only an indirect response to the thermal regime. The activity of biting flies (*Tabanidae*) increased as the thermal environment became warm. The wapiti responded to annoyance by flies by standing in ponds or open areas and by bedding among piles of creosote-treated posts which apparently repelled insects. Local ranchers in the area have noticed similar responses by cattle.

In habitat mosaics in which forage components fluctuate spatially and temporally, the optimal foraging pattern is one in which all components are sampled continuously yet maximum allocation of effort is to the type offering the greatest abundance of high quality food items (Pyke *et al* . 1977). Wapiti appeared to follow this strategy as predicated by changes in plant phenology and snow conditions. It was evident in the early spring when wapiti shifted rapidly to plant communities which offered the earliest available meristematic tissue, a pattern which other authors also have

noted (Knight 1970, Hunt 1979). The strategy was seen in late summer when the wapiti responded to grass maturation and a decline in abundance of forbs by shifting to foliage. Again during the winter, wapiti readily shifted from grazing to browsing as snow conditions dictated. During any season, however, all cover types were sampled by the wapiti. This pattern is adaptive in fluctuating environments in which areas having high food abundance or quality at one time may have a low abundance at another time and vice versa. By continuously sampling all cover types the wapiti is able to track changes in its nutritional environment and adjust its occupational patterns accordingly (Mackie 1970).

Snow cover affects distributions, by mechanically impeding movement and by altering forage availability. Snow depths required to affect movement are in the range of 50 to 60 cm (Gaffney 1941, Leege and Hickey 1977). These levels were not reached but this study indicated that snow cover less than 20 cm affects foraging patterns only slightly, depths greater than 30 cm effect a major shift from grazing to browsing.

By simply recording habitat occupation for foraging there is a risk of misinterpreting the effect of snow on food habits. Although in early winter wapiti responded to the presence of snow cover by foraging in the forest, this cover type was not used primarily for browsing. It was not until snow depths exceeded 30 cm that wapiti used the forest for this purpose.

Wapiti exhibited an innate tendency to graze which was evident in an overall preference for meadows or open areas compared to forests. It was expressed in late winter when animals grazed heavily in limited patches of snow free meadow. Evidence of this preference was also observed in the spring when they grazed almost exclusively on graminoids and forbs in meadows despite the abundance of shrub and tree foliage.

In general, the wapiti is a versatile and opportunistic herbivore which consequently is able to utilize a wide range of biomes (Murie 1951). Geist (1979) postulated that the wapiti, a recent arrival to North America, has had insufficient time to adapt to any particular niche or specialized life mode. Despite the fact that certain sub-species (*C.e. nannodes* and *C.e. roosevelti*) do exhibit morphologic tendencies towards specialized feeding styles as indicated by their dentition (McCullough 1971), the North American wapiti is indeed little different from the old world wapiti types (Geist 1971b).

Chapter 5

WEIGHT DYNAMICS

INTRODUCTION

Changes in body weight are expressions of energy and nutrient balances and reflect attempts by the animal to use resources to best advantage. Optimal deployment of resource use behaviours is particularly important in seasonally stochastic environments in which availability of nutrients and energy costs vary widely.

In temperate regions wild ruminants must capitalize on temporally concentrated food supplies in order to deposit sufficient tissue energy to subsidize maintenance during periods of resource scarcity and harsh weather. Mature males must deposit adequate tissue reserves to subsidize energetically costly breeding activities leaving sufficient reserves for winter when maintenance costs will not be met by the diet. Mature females must attain a level of condition which will enable them to survive submaintenance nutrient consumption and produce viable offspring (Thorne *et al* . 1976). Lactation constrains the ability of the female to rapidly achieve adequate tissue reserves during periods of nutritional abundance.

The wapiti is a generalist herbivore which exhibits diverse food habits and habitat preferences and is highly opportunistic in its resource use behaviour. Opportunism is expressed in seasonal migrations (Knight 1970), in taking

advantage of locally abundant and temporal food resources and in diverse food habits (Kufeld 1973). Its opportunistic nature should enable this species to shorten the annual period of negative energy balance more than is possible by specialist herbivores like the moose (Stewart *et al* . 1977).

This chapter examines weight dynamics of wapiti in relation to age, reproductive status, and certain seasonal factors in the environment.

METHODS

Weight Measurement

The elk were assembled periodically in a handling facility designed to minimize stress and risk of injury to either the animals or the handler. Body weight was measured using an electronic platform scale. Feed and water were not withheld so that body weights also included rumen fill.

Weights of pregnant cows were adjusted for weight of the gravid uterus using data reported for singly-conceived cattle (Eley *et al* . 1978), domestic sheep (Rattray *et al* . 1974), and white-tailed deer (Robbins and Moen 1975). For these species the weight of the fetus at term represents an average of 57% of the weight of the total gravid uterus. For an elk calf weighing 18.2 kg at birth the weight of the gravid uterus would be 31.89 kg.

Using data for sheep and white-tailed deer an equation was developed for relating percent of maximum uterus weight to the percent stage of gestation. The percent weight of the

gravid uterus was estimated from the equation:

$$\text{Log } Y = .0499X - .0189 \quad (r^2 = .955)$$

where Y = percent maximum uterus weight and X = % days of gestation. This weight was subtracted from total body weight giving the corrected body weight.

Fecal Analyses

To gain an impression of seasonal changes in forage quality consumed by wapiti, five to nine feces samples were collected over a one- or two-day period during 2 - 4 week intervals throughout the study. Samples were frozen until analysis. Crude protein (N x 6.25) content was determined using the macro-Kjeldahl procedure (A.O.A.C. 1965).

Statistical Methods

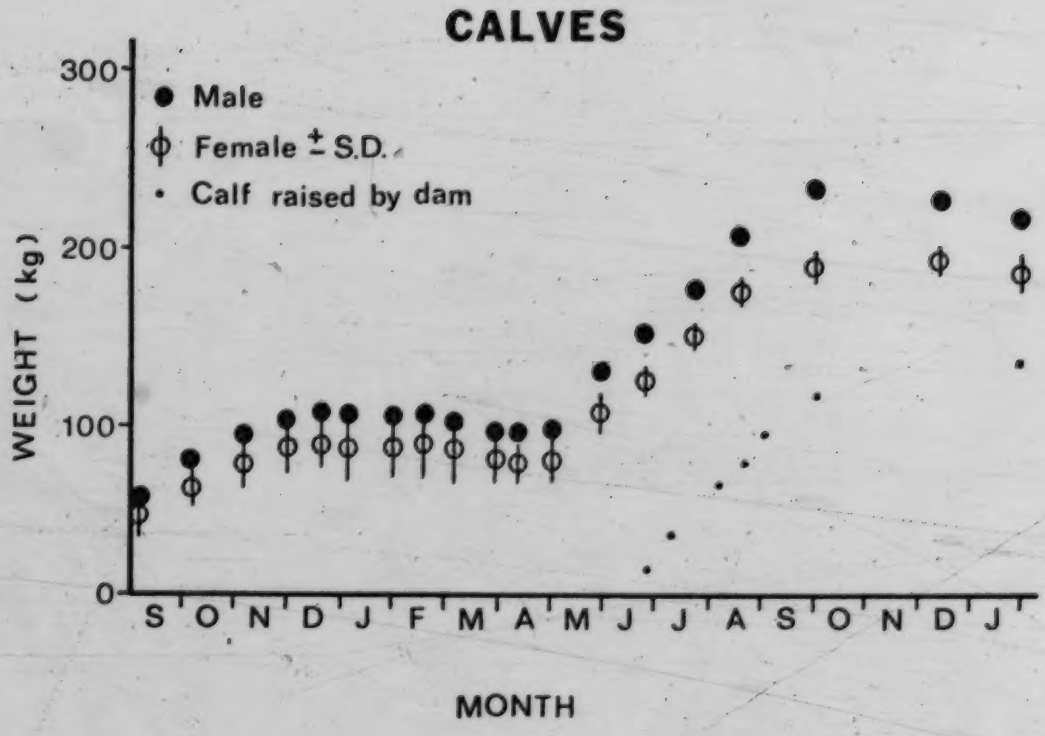
Differences in percent weight gain or loss between age and sex cohorts were analysed using Student's t-test (Sokal and Rohlf 1969) after logarithmic transformation. Linear regression was used to derive relationships between average feces crude protein content and rate of gain for calves and bulls.

RESULTS

Growth of Calves

After introduction into the enclosure in early September, the elk calves gained weight until late December (Fig. 5.1). The male calf experienced an 89.2% increase in weight at an average rate of 0.44 kg per day. Similarly, female calves gained 91.5% over their initial weight at an

Figure 5.1 Seasonal weight dynamics of male and female hand raised calves and a naturally raised calf. The mean weight of three female calves is shown with plus or minus one standard deviation.


CALVES
300
200
100
0
WEIGHT (kg)
Male
Female ± S.D.
Calf raised by dam
S O N D J F M A M J J A S O N D J
MONTH

average rate of 0.37 kg per day. The percentage increase in body weight of calves was significantly greater than for cows ($P<.001$) or for bulls ($P<.001$) (Table 5.1). The calf reared naturally the following year achieved a peak weight of 134 kg which was 29 kg above that of the hand reared male calf in its first fall season.

After late December 1977, the calves ceased growing until early May when spring forage first appeared. In the intervening period they lost an average of -9.9% of their peak weight . Percent weight loss in calves (-0.6 kg per day) was significantly less than for cows or for bulls.

During the spring and summer the calves (then yearlings), gained rapidly. Between May 2 and August 20, females grew at an average of 0.85 kg per day, and underwent weight gains averaging 118.6%. During the same period, the male experienced a weight gain of 114.4% (1.01 kg/day). Gain of female yearlings was significantly greater than for cows or for bulls. The maximum weights recorded for the yearlings occurred in October 1978. By December and January winter weight loss commenced.

The calf raised by its dam achieved a remarkable rate of growth of 1.08 kg per day between its date of birth (June 25) and August 20. Its birth weight was 18.2 kg and by August 20 had reached 78.6 kg. This calf continued to grow, though at a reduced rate until January 31, 1979, when the last weights were obtained.

Table 5.1. Weight changes of wapiti in different periods of the year.

Period	Age-sex Cohort: Calves % Change	Calves Rate (Kg./day)	Cows* % Change	Cows* Rate (Kg./day)	Bulls % Change	Bulls Rate (Kg./day)
Fall-Early Winter (September 1 - December 21, 1977)	93.9	0.39	9.4	0.16	5.8	0.11
Winter-Early Spring (December 21, 1977 -May 2, 1978)	-9.9	-0.06	-21.3	-0.35	-16.9	-0.28
Spring-Summer (May 2, 1978- August 20, 1978)	118.6*	0.85	37.0	0.57	48.0	0.86

* Weights corrected for gravid uterus weight.

* Male calf not included.

Growth of Cows

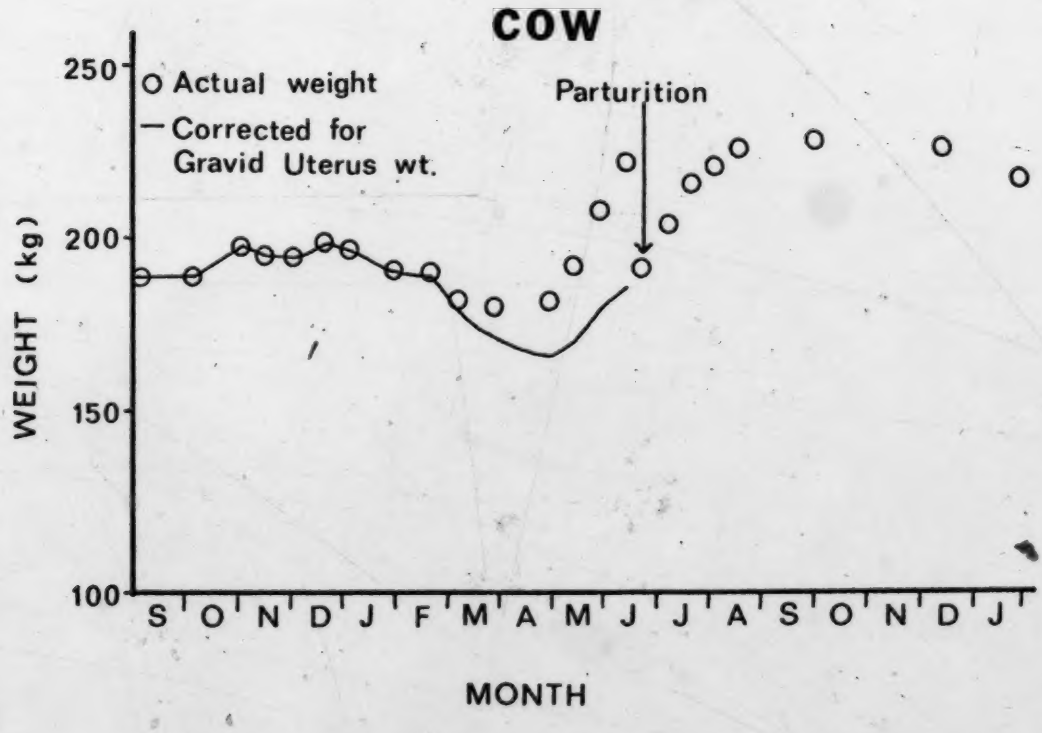
Peak weights (212 kg) were recorded on December 21, 1977. This represented an average gain of 9.4% since the time of introduction. Over the winter (December 21 to May 2) the cows lost an average of 21.3% of their peak body weight (corrected for weight of the conceptus). This did not differ significantly from weight loss incurred by bulls (Table 5.1).

By the end of March, the weight of the gravid uterus began to be a significant component of actual body weight (Fig. 5.2). Although the actual weight of the cow remained relatively constant between the beginning of March and the start of May, there was a loss in weight of maternal tissues (-13.3%). Over the same period the bulls lost an average of 7.0%, which was significantly less than that of the cows. Presumably the difference was a result of loss of maternal tissue as a consequence of the accelerated demands of the rapidly growing fetus.

Calves were born on June 15, 20 and 25, 1978 to each of the cows. Between June 25 and August 20, the cows gained an average of 14.4% at a rate of 0.51 kg/day while the bulls gained significantly more, 23.4% at a rate of 0.99 kg/day. The difference could have been due to the cost of lactation.

After the end of August, the cows experienced little growth. The mean weight on August 20 was 229.0 and increased to only 233.9 kg (0.11 kg/day) by October 3 1978, which was their peak weight for that year. During the period August 20

Figure 5.2 Seasonal weight dynamics of a cow wapiti. Change in non-pregnant body weight is indicated by a solid line.


COW
250
200
150
100
WEIGHT (kg)
Actual weight
Corrected for
Gravid Uterus wt.
Parturition
S O N D J F M A M J J A S O N D J
MONTH

to October 3 the female yearlings gained an average of 9.57% which was significantly greater than the 2.18% gained by the cows ($P<.02$). This may have been due to the additional cost of lactation. However the performance of these two cohorts may not be strictly comparable due to possible effects of age. Weight increments of the female yearlings in 1978 and 1977 were similar during the fall to early winter period.

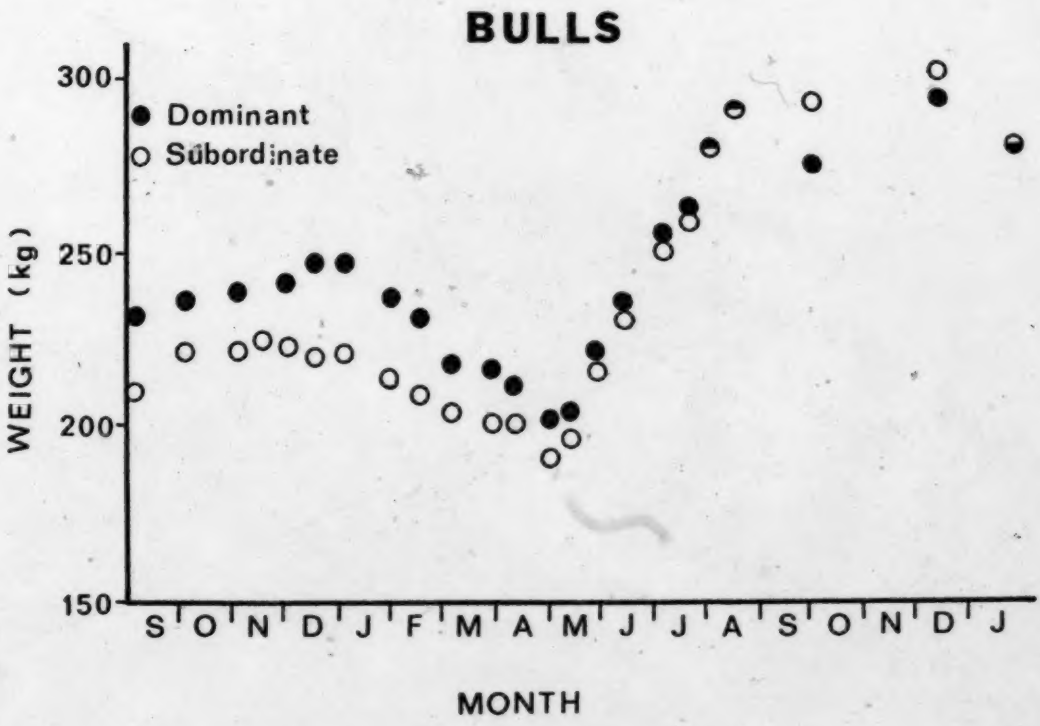
Growth of Bulls

Following introduction in 1977, the two yearling bulls gained weight until December (Fig. 5.3). On average they gained 5.8% of their initial weight. This did not differ significantly from the yearling cows. The peak weight of the dominant bull was considerably greater than that of the subordinate bull.

Over winter (December 21 to May 2) bulls lost an average of 16.9% of their peak fall weight. During the spring and summer (May 2 to August 20) the bulls gained 0.86 kg/day and achieved an increase of 48% over their initial spring weight.

While there was a considerable difference between weights of the dominant and subordinate bull in the fall of 1977 and subsequent winter, their spring and summer weights were very similar. This did not however alter the dominance hierarchy. In mid-August the bulls stripped velvet and polished their antlers. While both bulls were aggressive and dangerous during the next 40-day period, the dominant bull was notably more so than the subordinate.

Figure 5.3 Seasonal weight dynamics of wapiti bulls.


BULLS
300
250
200
150
WEIGHT (kg)
Dominant
Subordinate
S O N D J F M A M J J A S O N D J
MONTH

Growth ceased in both bulls during the rutting season. The subordinate bull remained at a relatively constant weight between August 20 and October 3, but the dominant bull lost 16.8 kg at a rate of -0.38 kg/day. After the rut both bulls gained weight until December 17. The subordinate's weight increased to 301.4 kg. The dominant bull recovered the entire loss it experienced during the rut, increasing his weight to 294.1 kg.

Influence of Environmental Factors

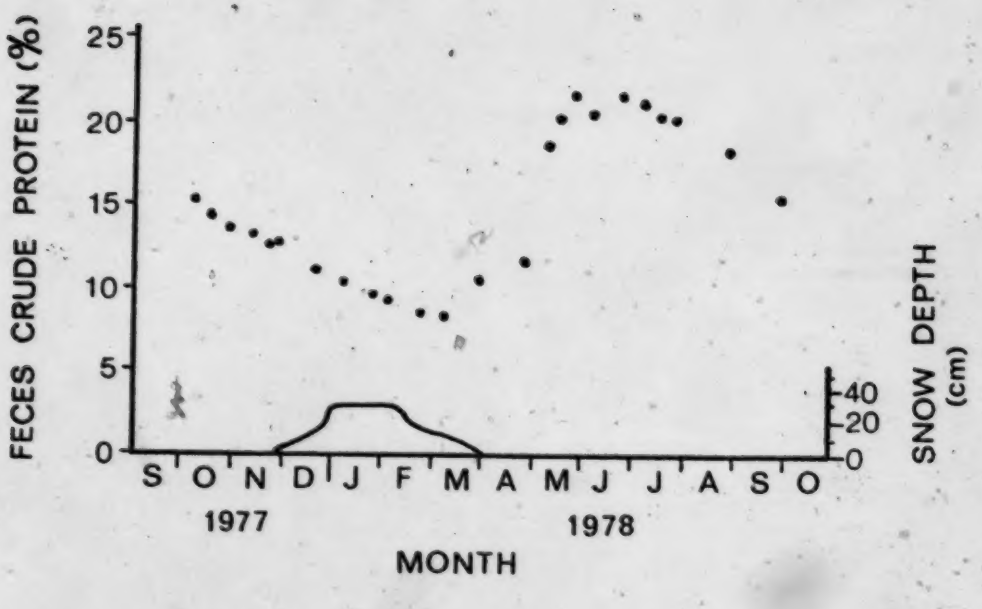
Many environmental factors affect the energetic status and hence weight dynamics of free-ranging wapiti. Forage quality and availability as affected by range and snow conditions, thermal stress, and disturbance are generally considered the most important influences. Among these it was possible only to investigate the effects of forage quality and biting insects.

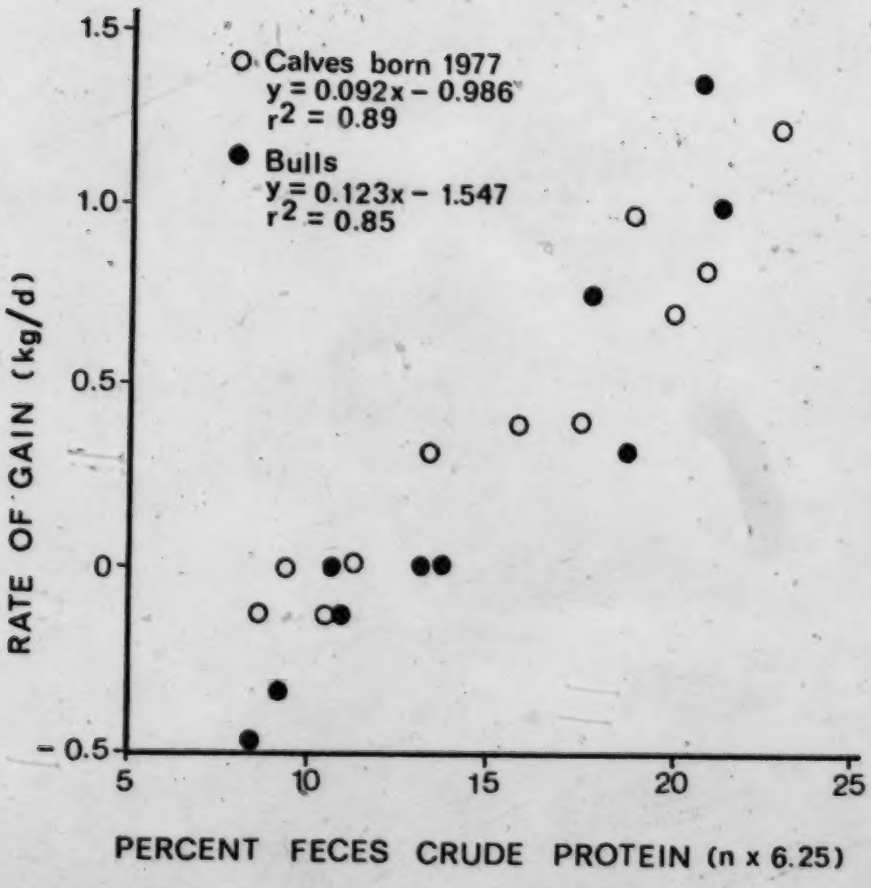
Forage Quality

The quality of herbage available to the elk varied seasonally with plant phenology and snow conditions. The consequent pattern of diet quality was reflected in the crude protein content of feces (Fig. 5.4). Fecal protein declined steadily throughout the fall and winter but began to rise with the disappearance of snow cover in late March. By April 25 the wapiti were beginning to feed on fresh forage, primarily in sedge wetlands. However, they continued to lose weight until after May 2 when new growth forage became abundant. Fecal protein

Figure 5.4 Seasonal variations in crude protein content (%) of wapiti feces.

Figure 5.5 Relationship between average daily gain and feces' crude protein (forage quality indicator) for wapiti calves and non-rutting bulls.


FECES CRUDE PROTEIN (%)
25
20
15
10
5
0
40
20
0
SNOW DEPTH (cm)
S O N D J F M A M J J A S O
1977
1978
MONTH


Calves born 1977
y = 0.092x – 0.986
r2 = 0.89
Bulls
y = 0.123x – 1.547
r2 = 0.85
RATE OF GAIN (kg/d)
1.5
1.0
0.5
0
– 0.5
5
10
15
20
25
PERCENT FECES CRUDE PROTEIN (n x 6.25)

and growth rates of the elk remained high until late August.

The relationship between average daily gain and feces crude protein was investigated for female elk calves born in 1977 and bulls (Fig. 5.5) excluding data from the rutting period. Due to the additional energetic costs of pregnancy and lactation, cows were excluded from this analysis. A strong relationship between average feces crude protein (%) and rate of gain was determined for bulls (r^2 = .85) and for the elk calves (r^2 = .89).

Insect Harassment

During the month of June the wapiti were frequently subjected to intense insect annoyance. The animals responded by altering feeding patterns and habitat use. The effect on growth is evident in Table 5.2. In both yearling females and bulls, rates of gain were significantly less during the period of insect harassment. The effect on the yearling male was obvious as well. For all of these age/sex cohorts, rate of gain dropped by an average of 54% during the month of June compared with the immediately preceding two-week period.

DISCUSSION

Weight change is an expression of a number of interacting factors including nutrient intake, energy expenditures, physiological status, and body compositon.

Table 5.2 Influence of insect harassment on rate of gain of yearling and bull wapiti. Significant differences between the period of intense insect harassment and the preceeding and succeeding two-week periods (t-test) are indicated by asterisks.

	Mean ADG* of Yearling females (kg./day)	Mean ADG of Yearling Male (kg./day)	Mean ADG of Bulls (kg./day)
2 weeks before	1.18 ± .03**	1.49	1.38 ± .07***
Period of Insect Harassment	0.68 ± .15	0.87	0.67 ± .02
2 weeks after	1.16 ± .13*	1.20	1.03 ± .06***

*P<.02, **P<.01, ***P<.001
*Average Daily Gain

However, weight may be an unreliable indicator of energy status since changes in body mass can be due to variations in a number of carcass constituents, water, rumen fill, bone, protein or fat. Holter *et al* . (1979) outlined factors which determined the composition of weight change in white-tailed deer. The extent of fat or protein deposition or mobilization varied with body weight, age or season, digestible energy intake and digestible nitrogen intake. Nutritional demands for growth of other tissues such as antlers and pelage and the demands of gestation and lactation also influence the magnitude and form of energy storage or mobilization.

Seasonal weight dynamics of elk followed a pattern which was correlated with variations in certain seasonal environmental parameters. Diet quality, a function of forage quality and availablity, appeared to be a major determinant. This parameter was influenced by plant phenology and snow cover, and probably by weathering in late winter and early spring.

Diet quality declined in the fall and rates of gain were correspondingly lower. Continuation of weight gain in the fall enhances energy reserves for the ensuing period of negative energy balance. In this study the elk began to lose weight after arrival of heavy snow cover in late December. This period coincided with fecal protein levels of about 10%. Although snow cover receded in late winter and early spring, loss of weight and body condition continued until

the initiation of herbage growth in early May. On this basis the apparent duration of negative energy balance was about 131 days. In comparison the average estimated annual duration of negative energy balance over an 18-year period for moose was 225 days (Stewart *et al* . 1977).

Seasonal changes in energy expenditure were not quantified. The energy costs of locomotion and thermoregulation likely increased in the winter as a result of snow cover and low temperatures. Voluntary restrictions in feed intake may also have influenced winter weight loss. This phenomenon has been demonstrated in captive caribou (McEwan and Whitehead 1970) and in white-tailed deer and mule deer (Silver *et al* . 1969, Wood *et al* . 1962), despite availability of adequate feed. However this has not yet been demonstrated in elk. On the contrary, it appears that elk are able to maintain or increase weight over winter if supplied with adequate feed (Dean *et al* . 1976).

Physiological status also appeared important. Body composition at peak fall weight may play a role in determining the extent of over winter weight loss. While older animals accumulated extensive fat stores, moose and caribou calves entered winter with smaller reserves (Dauphine 1976, Stewart *et al* . 1977). Catabolism of a unit weight of tissue in a calf would consequently yield less energy than one unit in an older animal. It is possible that calves minimize weight loss to a greater extent than older animals by foraging more selectively and by supplementing

forage intake as long as possible with milk. Weight loss in elk calves was significantly less than that experienced by yearling bulls and pregnant cows in this study.

Reproductive status played an obvious role in weight dynamics of mature males. The dominant bull at the age of two and a half years lost considerably more weight during the rut than his subordinate. Social status is thus apparently correlated with the extent of depletion of tissue energy reserves during the rutting season. Unless recovery following the rut is possible due to favorable foraging conditions, as occurred in this study, depletion of energy reserves during the rut may adversely affect survival in the subsequent winter period. The appropriate behavioral strategy which would maximize reproductive fitness would therefore represent a compromise between participating in one rut and sparing energy reserves to ensure survival to the next.

Reproductive status of cows also had marked effects on weight dynamics. The demands of late pregnancy and lactation depressed body weight gains. Rapid growth of the fetus was estimated to begin in mid March. This meant that the cows had to compensate for an additional demand on energy stores for six to seven weeks until diet quality improved with emergence of new growth herbage at the beginning of May. Prior *et al* . (1979) suggested that during pregnancy, fetal and maternal tissues compete for available nutrients and that when the supply is limited fetal tissues have a higher

priority than many maternal tissues. Consequently, during this period the cows mobilized tissues rapidly. However, during the remaining four to five weeks of gestation, high quality herbage was abundant and the cows apparently were able to recover much of the winter weight loss.

There is an obvious adaptive advantage to timing late gestation with a period of nutritional abundance considering the serious impact that maternal weight loss can have on neonatal birth weight and subsequent survival in elk (Thorne *et al* . 1976). Both weight loss due to the products of gestation and birth weight of the one calf weighed in this study were comparable to the weights in wapiti maintained by Thorne *et al* . (op cit.) on a high plane of nutrition throughout the winter and spring.

The rate of gain of the maternally raised calf was much higher than predicted by a regression equation relating rate of gain of a calf to average maternal weight (225 kg) for a large number of ungulates and subungulates (Robbins and Robbins 1979). The growth of the calf was prolonged at least until the end of January 1979 when the last weights were obtained. This was likely only possible as a result of prolonged milk consumption.

Wapiti are adapted to marginal subsistence during winter as a result of versatility and flexibility in food habits and occupational patterns which permit them to extend the period of positive energy balance late into the fall and to capitalize on the most available and nutritious forage

items throughout the year. However, they depend on full nutritional recovery during the summer to prepare for demands of body maintenance and reproduction in the following autumn and winter. Short (1975) concluded that winter survival of white-tailed deer depends heavily on good nutrition during late summer and early fall. Any disruptive factor, physical or biotic, which results in a decrease in feeding time or a decreased efficiency in use of that time, or increases energy expenditure is potentially detrimental. This is especially true preceding or following harsh or prolonged winters with early snow cover or late green-up. The presumed influence of insect harassment in this study was expressed in reduced growth rates and if sufficiently intense or prolonged could have resulted in a shortfall on target fall weights. Prolongation of such a disruptive factor could seriously affect reproductive success and/or survival. In light of this possibility wildlife managers should consider the potential disruptive impacts of human activity.

Chapter 6

SYNTHESIS

Much of the ecology of the wapiti and other large herbivores can be understood in terms of energy flow. Geist (1979) states that, "Bioenergetics makes it evident that energy is difficult to obtain, expensive to process and all too readily lost. Therefore individuals must live frugally, stay in predictable social and physical environments which contain a minimum of costly surprises, and communicate with minimum effort in such a manner as to reduce the cost of direct competition."

Energy acquisition is an important limitation for large herbivores. While the resource they exploit is abundant it is frequently and periodically of very low nutritive quality during a significant portion of the year. During seasons when high quality forage is abundant the wapiti must consume sufficient amounts to insure adequate energy stores which will subsidize energy intake during the more limiting seasons. In such periods of abundance the large herbivore must gain weight at a rate which will enable it to achieve a level of energy storage at the start of the period of negative energy balance which will insure its survival and adequate reproductive performance until resources again become less limited.

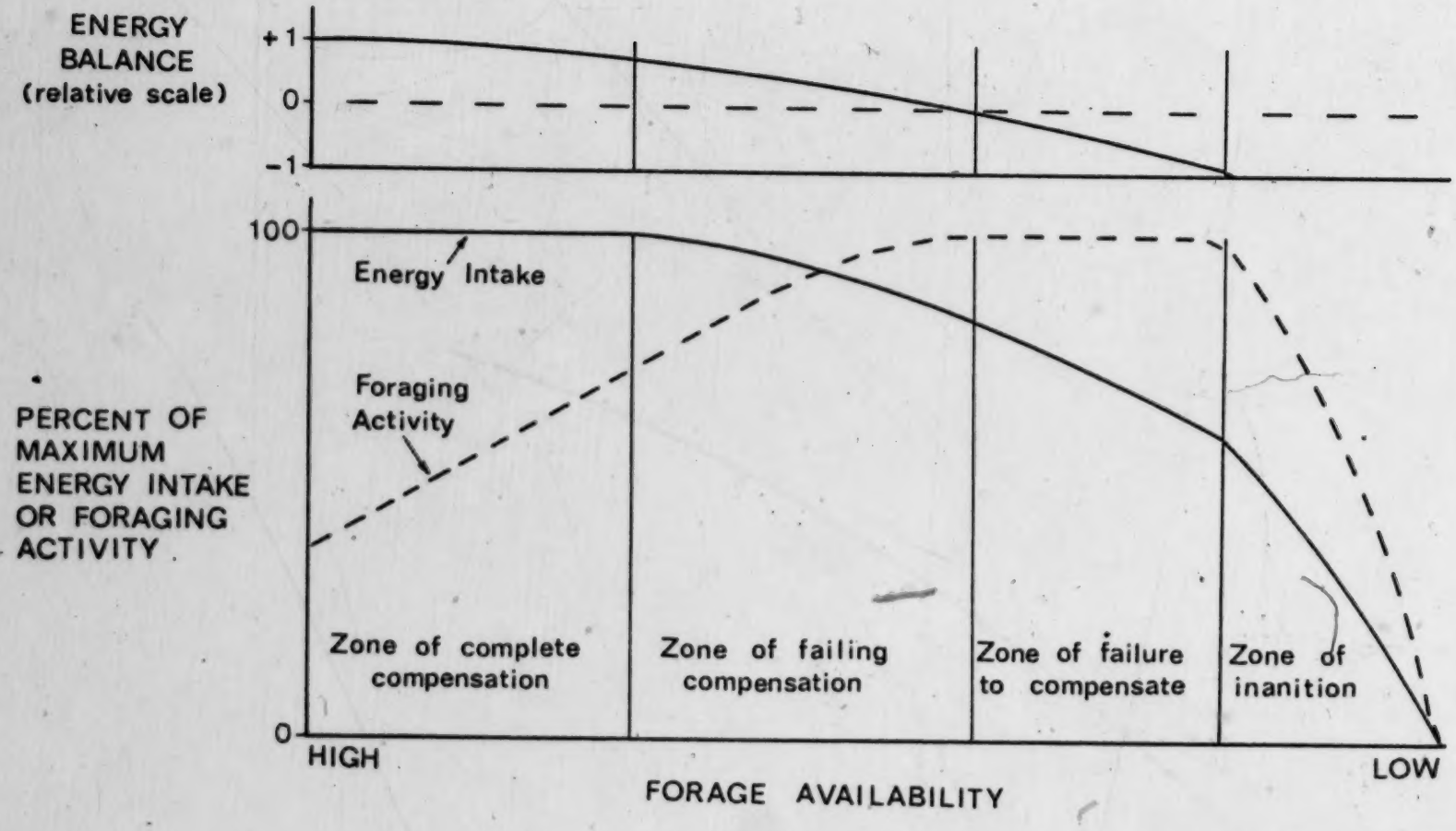
In a versatile, generalist herbivore like the wapiti this means that it should capitalize on the first available nutritious forage in the spring, feed selectively on the

highest quality forage available when forage is superabundant and follow the principle of energy optimization in diet selection and habitat patterns as resources again become more limiting through the fall and into winter.

One of the most critical interactions occurring between a large herbivore and its environment is its ability to compensate for declining forage availability by increasing foraging effort, of which time spent foraging is a measure. The relationship is represented diagrammatically in Fig. 6.1. As forage availability declines the animal is able at first to compensate by increasing its foraging effort. In this zone of compensation energy balance can be maintained at a high postive level though it begins to decline slightly due to additional expenditures related to increased activity. As the animal increases foraging time with further declines in forage availability it no longer is able to compensate fully. Consequently energy intake and retention both begin to decline (zone of failing compensation). Foraging time eventually approaches a maximum level which is determined by physiological limitations such as the rate of passage of digesta or constraints related to the need to engage in other essential activities. Once foraging time reaches a peak it continues to remain high for some time despite the failure to compensate for additional energy expenditures.

The animal begins to experience negative energy balance

Figure 6.1 Diagrammatic representation of the relationship between energy intake, foraging time and energy balance.


ENERGY BALANCE (relative scale)
+1
0
-1
100
0
Energy Intake
Foraging Activity
PERCENT OF MAXIMUM ENERGY INTAKE OR FORAGING ACTIVITY
Zone of complete compensation
Zone of failing compensation
Zone of failure to compensate
Zone of inanition
HIGH
LOW
FORAGE AVAILABILITY

which in cold environments is compounded by thermal losses. Eventually energy reserves become taxed to the point where the animal may give up, i.e., reduce foraging activity or finally cease feeding altogether. At this point maintenance costs are solely met by catabolism of body tissues. Such a state cannot last long.

Exposed to seasonal environments in which thermal conditions and habitat and food resources vary in time and space, the wapiti has evolved mechanisms which maximize its fitness to survive and reproduce successfully. While this is achieved in large part by optimizing energy balance on both daily and annual bases there are constraints to which the wapiti is subject. It must expend energy for reproduction to maintain its social status and to maximize its genetic output, despite the heavy burden this places on proximate energy demands. It must avoid being preyed upon. In addition there may be specific required nutrients which it must consume in adequate amounts. These and other factors can modify the efficiency of energy flow.

Once these constraints are recognized, it is seen that the wapiti has a number of options. It must decide which habitats to occupy, with what frequency and duration. It must decide how to allocate its time to any array of often mutually exclusive activities which vary in their energetic costs. It must decide what food items to include in its diet and with what frequency. Finally it must integrate all of these options into a selective pattern of time allocation

and resource use behaviour which optimizes short term daily energy balance, yet keeps it in phase with a seasonal cycle relative to seasonal shifts in abundance of resources and costs of existence and reproduction. The adeptness with which they do this is reflected in weight dynamics as an indicator of gains or losses, savings or expenditures, of body tissue energy stores.

The seemingly infinite array of behavioural sequences and specific resource use patterns that ungulates engage in is at first confusing in variety. The challenge of behavioural ecologists is to discover common denominators and to explain deviations on the basis of local conditions. By detailed study of animal-environment interactions and research on specific animal functions like thermal physiology or digestion and energy expenditure for activities and maintenance, we move closer to being able to predict behavioural patterns and animal performance in the natural environment. Particularly in this day when assurance of existence of many animal populations in increasingly altered environments rests on sound management programs, it is essential to have adequate knowledge of animal functions and responses to the environment. There is a need for a great deal more research in this field of study to provide information which will permit us to replace the largely empirical approach we must now use to predict human impacts and animal behaviour and to manage wildlife resources.

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Appendix 1

Rearing and Management of Wapiti Calves

Introduction

The use of captive raised wild ungulates in research is becoming more common. There are many advantages to working with tame, tractable animals for studies in nutrition, physiology and behaviour. Habituation to human presence, handling procedures, and experimental apparatus is enhanced by hand-rearing.

While there are numerous reports on successful rearing programs for a variety of species (Murphy 1960, Long *et al* 1961, Wood *et al*. 1961, Schwartz 1976, Regelin *et al*. 1979), many problems are commonly encountered. Respiratory and enteric diseases are caused by a variety of pathogens (Nagy *et al*. 1971). Other areas of frequent concern are adequate milk formulation and level of feeding (Blaxter *et al*. 1974), weaning strategy and subsequent nutrition (Regelin *et al*. 1979), and training for experimental purposes (Mattfeld 1973).

Since some of these concerns are more serious with certain species than with others, it is useful to have access to species-specific reports on artificial rearing and training when designing research programs. This report deals with the techniques used and problems encountered in hand

rearing eighteen wapiti calves. The program was carried out at the Edmonton Research Station, University of Alberta.

Study Animals

Wapiti calves were obtained from a number of sources. In June 1976 nine were acquired from the Sybille Research Station in Wyoming. Five calves were born to captive wild cows held in Edmonton in 1976 and four more were born in 1977. The calves ranged from 1 to 36 hours old when collected.

Management and Training

The first task is to train the calves to feed from a bottle. The ease with which a calf accepted bottle feeding was related to its age. Most rapid acceptance was achieved with calves under six hours old. In the present work, a calf about an hour old suckled the bottle after only 10 minutes exposure to handling.

After six to eight hours post-partum, it appeared that calves were afraid and refused to accept feeding for up to several days. It is possible that after eight hours species identity or maternal identity had crystallized as a result of maternal care. In calves collected after this critical period, much patience was required to overcome fear of

humans. It was best for one handler to train a calf. Trust was gained by quietly sitting with the new calf in a small area isolated from extraneous disturbances. When the calf began to raise its head from the hiding-prone posture, this was an indication it was losing its fear of the handler. By gently and cautiously rubbing the calf with a warm damp cloth once this stage was reached, habituation was accelerated. Once the calf was no longer reacting fearfully when touched, bottle feeding was attempted. We used a sheep nipple on the bottle which contained a sufficiently warm formula. It was usually necessary to cut a larger hole in the nipple to permit an adequate flow of milk. The nipple was placed in the side of the mouth through the diastema and squeezed to introduce a little milk. The calf eventually began to suckle if it was not afraid.

Most calves responded after a few hours but some persisted in refusing to suckle. In the first year of the program, intubation and drenching was employed to sustain life. A number of calves subsequently totally refused the bottle probably because of these forceful tactics. Of the five which consistently refused, three died and two others were force fed until 28 and 74 days of age, respectively. The former finally began to suck from a bottle while the latter was force fed until weaned. In the second year, a more patient approach resulted in all calves accepting bottle feeding within 24 hours of being collected.

Neonates were housed individually indoors in clean quiet surroundings with deep straw bedding until they were habituated to the rearing program. This procedure enhanced training and minimized the transfer of disease. If given the opportunity, a hungry neonate often attempted to suckle another calf rather than accept bottle feeding. This can impair habituation and the physical stimulation of the other calf often resulted in defecation and soiling of the hungry calf.

Once the calves were bottle-trained and had lost fear of the handler, access was allowed to a dry clean pasture area with good plant cover and shelter. This permitted them to exercise and to begin to pick at forage items and eat soil, all of which are essential for maintaining health and getting them started on solid feed.

While well-nourished calves are hardy, it is important to avoid exposing them to cold wet weather. When they were maintained out of doors, a suitable shelter with dry bedding was provided and the calves were penned in it during inclement periods and at night.

Gentle directive persuasion was the most successful means to acquire cooperation. Halter training was initiated early when the animals were 2 to 3 weeks old. If training was left until they were larger, there was a greater risk of

injury due to struggling. Snug webbing halters are recommended over self tightening halters which frightened calves and made training difficult. Loose halters could not be left on since calves occasionally caught a hind foot in them while scratching. Halters were put on several days prior to the initial training period.

Long lead shanks made of 5/8" rope with quick release snaps were most suitable for training. The use of force at any stage should be discouraged since frightened calves did not learn readily. Initial attempts at leading were conducted in a long narrow runway. The trainer capitalized on the desire of the calf to follow. This was best accomplished part way through a feeding period when the calf was only partially satiated and wanted to follow the bottle. The trainer walked away from the calf which then began to follow voluntarily. When the calf reached the bottle the lead shank was held short and pulled gently, then walking was continued. If the calf resisted, the tension was released and the procedure was repeated. Soon the calf learned to ignore the pressure and readily walked and sucked on the bottle.

In the second lesson, the above was repeated but the calf was then tied short to a post and fed the remaining portion of the bottle. The trainer then left the calf alone for several minutes so that it adjusted to the new

experience. It was then released using the quick snap and the handler walked away. If the calf had struggled there was no negative association with the handler. The lesson was repeated until the calf learned not to struggle when tied to the post.

The next stage involved getting the calf to lead properly. A bottle was used initially for positive reinforcement. The lead shank was held about half a meter from the snap end and the long end was wrapped around the hind quarters of the calf then brought forward. Resistance to pressure on the halter at the short lead was countered by sharp jerks on the rope around the hind quarters. The trainer did not pull continuously on the rope as this invoked balking. Sharp jerks were usually sufficient to get the animal to move forward. If the animal became frightened, it was released or calmed by feeding or petting. Nervous calves often led properly with a long leadrope. Repetition and patience were essential if quiet cooperative animals were to be obtained. Using these procedures, wapiti were trained to walk into controlled environment chambers (Gates and Hudson 1978) and on a treadmill (Gates and Hudson 1979).

Handling Facilities

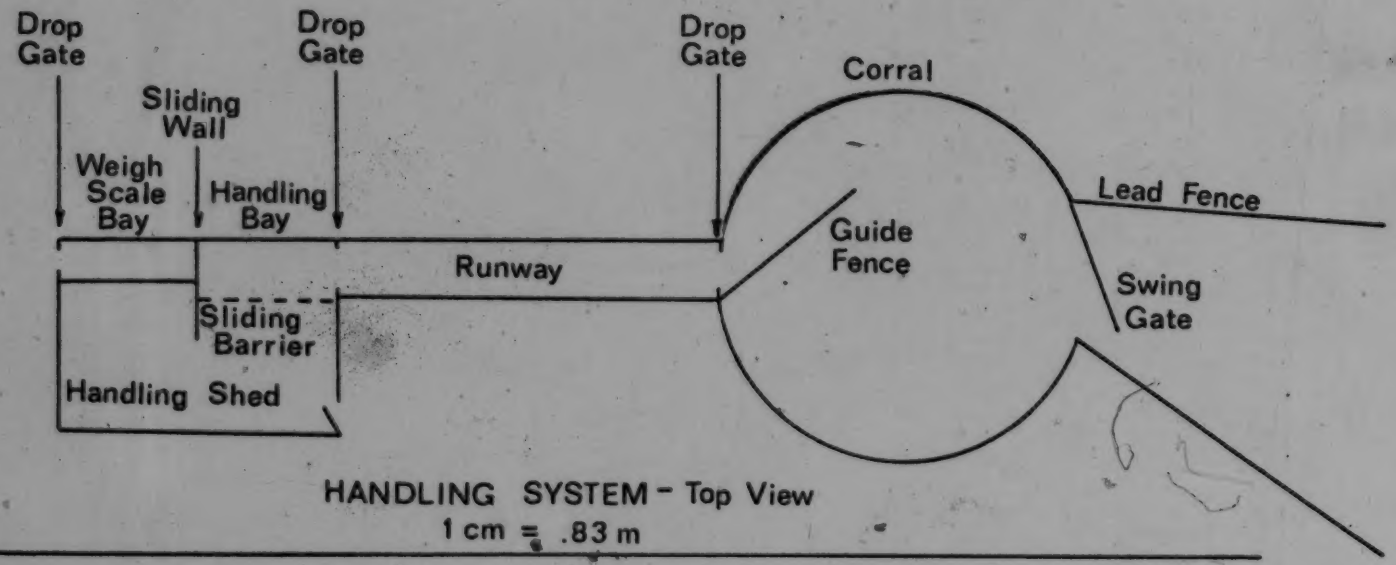
Handling facilities and experimental apparatus should be designed to minimize risk of injury to either handler or

subject. The cooperation of any subject, trained or untrained is best achieved by designing facilities which passively limit alternatives. High corrals, drop gates, and circular flow systems are important to minimize excitement. One system used with maximal success for collecting blood samples, measuring and weighing wapiti, moose and a mule deer fawn is illustrated in Fig. 1. The system was designed for handling semi-free ranging animals held in a 60 ha enclosure.

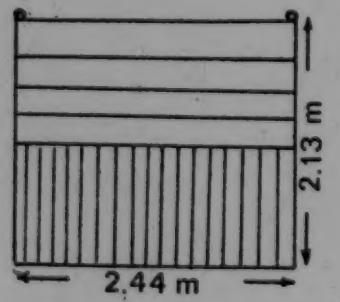
The animals were assembled in the circular corral then moved into the runway. The runway was sufficiently wide (1.3 m) to permit an adult wapiti or moose to turn around without injury. The fences were about 2.5 m high which was adequate for the semi tame animals in this study. A sliding barrier constructed of metal bars was pulled back prior to moving an animal into the handling shed. The shed could be kept dark by closing all ports. Hence, the animal was free to move around and to become accustomed to the facilities prior to handling. When it was quiet the barrier was pushed toward the animal which stood quietly against the wall. Blood samples and measurements could be taken from adult moose without further restraint, however it was necessary to use a halter on the wapiti.

After handling, a sliding wall was drawn back to permit access to a scale platform in the next bay. The animal was

Figure 1. A handling facility for cervids.



HANDLING SYSTEM - Top View
1 cm = .83 m



SLIDING BARRIER - Side View

weighed then released to the outside through the drop gate. Throughout two years of operation there were no injuries sustained by animals or researchers using this system.

Feeding

A range of milk substitutes has been used for artificial feeding of infant wild ruminants. The majority are based on cow's milk, either whole, condensed or powdered. Murphy (1960), Silver (1961) and Wood *et al.* (1961) used canned evaporated milk fortified with additives for rearing deer fawns. Schwartz *et al.* (1976) used a mixture of one part evaporated milk and four parts homogenized milk for pronghorn antelope fawns (*Antilocapra americana*). Red deer calves were successfully raised on homogenized cow's milk (Youngson 1970)

Although it is possible to use a range of substitutes, a number of workers agree that the choice of milk ration should be based on closest practical similarity of composition to mother's milk for that species (Kitts *et al.* 1956, Murphy 1960, Wood *et al.* 1961, Silver *et al.* 1961). For red deer, a close relative of wapiti, commercial ewe milk substitute resulted in excellent performance of calves (Blaxter *et al.* 1974) and success was attributed in part to the close similarity of ewe milk and red deer milk.

Two basic liquid rations were used to feed the calves in the present study. One consisted of a mixture of 0.44 l evaporated milk (1 can), 1.0 l whole milk and 0.07 l corn oil. The other ration was ewe milk replacer mixed with water to a concentration of 20% (W/W), 70 ml of corn oil was added per litre to increase the fat content. Initially calves were fed dairy colostrum. A good supply of colostrum was collected and stored frozen in anticipation of a calf rearing program.

Either of the base rations worked well for wapiti calves. A typical feeding schedule based on replacer is outlined in Table 1. On the day of birth the calf should be fed small amounts of colostrum, e.g. 200 mls, frequently. A night feeding should be included. Starting the second day, replacer is introduced to the diet. The proportion of replacer is increased gradually to 100% by day 20. On day 4 feeding frequency can be reduced from 5 to 4 times daily. The calves should be fed first between 7:00 and 8:00 A.M. and the last feeding should be no earlier than 9:30 to 10:00 P.M. After day 35, three feedings per day are sufficient. After day 50, the amount of milk fed can be reduced gradually and by day 56 only 2 feedings are necessary. Weaning can be done after day 80.

Fresh water, earth and forage was offered at all times. Wapiti calves began to consume foliage of some of the common

Table 1. Feeding schedule for wapiti calves.

Age (Days)	Intake (litres/day)	Number of feedings/day	Ration
1	1.0	5	colostrum
2	1.3	5	0.3 replacer 1.0 colostrum
3	1.3	5	0.5 replacer 0.8 colostrum
4	1.3	4	0.7 replacer 0.6 colostrum
5	1.4	4	0.9 replacer 0.5 colostrum
6	1.5	4	1.2 replacer 0.4 colostrum
7 to 9	1.6	4	1.4 replacer 0.2 colostrum
10 to 13	1.7	4	1.5 replacer 0.2 colostrum
14 to 16	1.8	4	1.6 replacer 0.2 colostrum
17 to 19	1.9	4	1.7 replacer 0.2 colostrum
20 to 35	2.0	4	replacer
35 to 50	2.2	3	replacer
51 to 55	2.0	3	replacer
56 to 60	1.3	2	replacer
61 to 70	0.8	2	replacer
71 to 80	0.5	1	replacer

browse species (e.g. willow or aspen) at an early age. The more rapid the transition to voluntary consumption of solid feed the less was the incidence of enteric disorders. The pelleted weaning ration used is described in Table 2. If animals were kept indoors, a pail of uncontaminated earth was on offer.

Until the calves were four weeks old, after each feeding the buttocks and area around the anus was sponged with a moist cloth to stimulate defecation. In naturally raised calves, the cow performs this task by licking the calf while it is nursing (Arman 1974).

Sickness, Losses and Treatment

Of the eighteen calves collected, only three failed to survive infancy. All of these had refused to accept bottle feeding and were extremely fearful of people. Two died after seven or eight days of apparent starvation and the third died of a suspected case of gastroenteritis. Poor condition likely contributed to its death.

Two calves died at about eight months of age. Their illness was characterized by a rapid onset of debilitating symptoms followed by death within four or five days. Both suffered severe intestinal hemorrhage which was manifested by bloody diarrhea. Numerous hemorrhages were present on the

Table 2. Composition of the post weaning feed ration.

Ingredient	kg/tonne
Alfalfa meal (minimum 15% Protein)	255
Barley (coarse ground)	310
Wheat Bran	140
Beet Pulp	135
Wet Molasses	70
Soybean Meal	85
Trace Mineral Salt	5
Include 1.32 kg Vitamin Premix:	
Vitamin A 4.54 x 10^6 IU/lb	
Vitamin D 5.675 x 10^6 IU/lb	
Viatmin E 4.54 x 10^6 IU/lb	

mucosal surface of the lower bowel. The lymph nodes appeared enlarged and contained excess fluid in one animal. There was no evidence of parasites upon examination of feces and bacteriological culture of several organs demonstrated no significant bacteria. No viral agents were detected. Histological evaluation of numerous organs revealed a diffuse inflamation of the walls of several blood vessels and marked leukopoenia was noted in a blood sample taken a day before death from one animal.

The marked tissue abnormalities noted on microscopic examination combined with the gross post mortem observations, clinical history, and lack of significant bacteriological or viralogical findings, indicated a severe viral infection which affected predominantly the blood vessels and immune system. The agent suspected to be responsible was the virus of malignant catarrhal fever. The observed clinical symptoms were suggestive of the preacute form of the disease (Daubney and Hudson 1936). It may have been contracted from domestic sheep which were held in pens adjacent to the wapiti. Domestic sheep may be asymptomatic carriers of this virus (Clark *et al*. 1970).

During the first year of rearing calves, diarrhea was a frequent problem until the calves passed four weeks of age. Once they began consuming a significant amount of solid feed, the incidence of scours was greatly reduced. Diarrhea

occurred on 55 out of 277 animal feeding days during the first 30 days of life or about 20% of the time. In contrast, during the second year diarrhea occurred only 5 out of 120 animal feeding days or 4% of the time. The difference was thought to be related to an improved feeding program based on experience gained in the first year and the inclusion of colostrum in the formula. Numerous studies have demonstrated the value of antibodies passively acquired from colostrum to the health and survival of the neonate (Campbell *et al.* 1977). Inclusion of bovine colostrum to bottle fed formulas may be important as well to wild calves raised in an unnatural environment even if they have had a chance to suckle from their dams during the first hours of life. Under conditions of captivity, the calf is likely to be exposed to infectious agents against which passive immunity supplied by the natural mother has no specificity. Without the addition of bovine colostrum, it must depend solely on natural immunity for protection. While broad spectrum anti-diarrhetic oral antibiotics were frequently and necessarily given as treatment in the first year, they were used on only two occassions in the second year.

In the first year, rations based on both commercial ewe milk replacer and whole-canned milk mix were fed. Some workers have personally expressed a dislike of powdered milk replacers and favor formulas based on liquid milk. Heat denaturation of whey proteins during the manufacture of

powdered replacers can alter the immunoglobulin content and clotting characteristics of milk proteins in the abomasum resulting in inefficient digestion and may predispose the calf to diarrhea (Roy and Ternouth 1972). The occurrence of diarrhea in relation to feeding liquid milk or replacer formulas was examined for the first 30 days of age for calves in the first year of the program. An analysis of the results is summarized in Table 3. There was no significant difference in the occurrence of diarrhea between the two formulas.

Initial treatment for diarrhea consisted of reducing the intake of milk or replacer for several meals but the volume fed was maintained by adding water. Electrolytes were also added to the ration. If this failed to work, the calf was administered a broad spectrum oral antibiotic mixed with its diluted formula, e.g. one which contained neomycin and sulfa drugs. Since dehydration from fecal water loss or reduced water intake is a feature of diarrhea (Fisher and Martinez 1976), every attempt should be made to maintain hydration and electrolyte balance. It is recognized that *Eschireshia coli* infections are often associated with feeding inadequate amounts of nutrients (Roy and Ternouth 1972), hence it is essential that a reduction in the amount feed should be of short duration.

Table 3. Occurrence of diarrhea in relation to the type of formula fed in calves up to 30 days old.

Type of Formula	Days on which Diarrhea was	Days fed	Expected Occurrence	x^2
Liquid Milk	15	72	14.30	.003
Ewe Replacer	40	205	40.71	.001

$x^2 = .004$

$x^2.05 = 3.84$

Conclusions

Wapiti calves are hardy and relatively easy to raise if adequate care is given. The three predominant problems encountered in the program were initial refusal to accept bottle feeding, high incidence of scouring and contraction of a viral disease. Early unwillingness to feed from a bottle is also a problem encountered in the closely related red deer (Blaxter *et al*. 1974, Youngson 1970) and may be a phylogenetic characteristic since neither moose nor North American deer fawns pose much of a difficulty in hand feeding (personal observation). The problem can be largely avoided by collecting calves before they are 6 hours old and/or by habituating them to a handler slowly and quietly before attempting to feed them.

The high incidence of scouring in the first year was reduced by more cautious feeding and by including dairy colostrum in the formula. Contact between domestic and wild stock should be strictly avoided in order to reduce the risk of transferring contagious diseases which could be more pathogentic to the valuable and hard to obtain captives.

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Appendix 2

Allometric Relationships

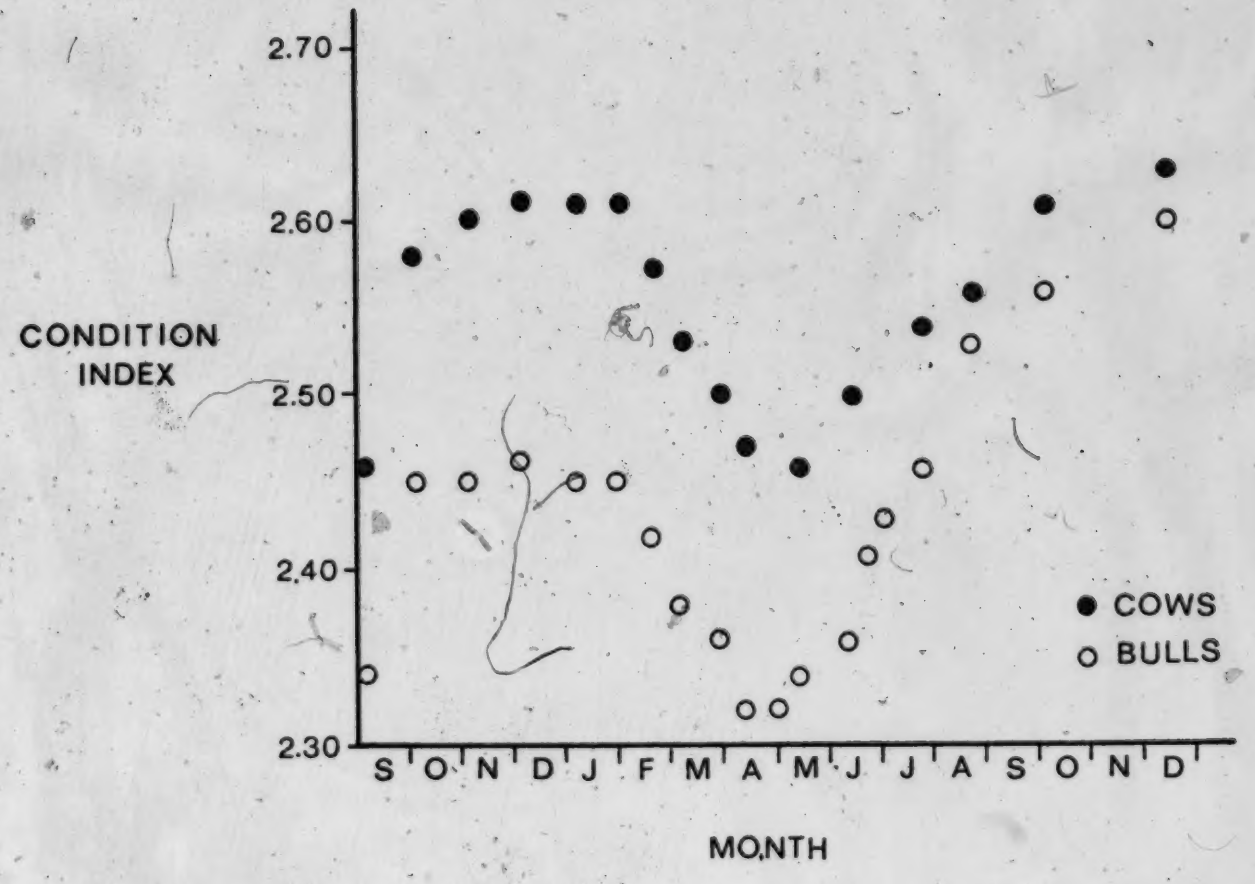
Seasonal Changes in a Condition Index

The ratio of chest girth to hind foot length served as an index of condition in cows and bulls since hind foot length did not change over the duration of the study in these animals. Hind foot length of cows averaged 57.3 cm and the bulls both had a hind foot length of 61 cm. Chest girth varied considerably with tissue depletion and hair coat changes.

Seasonal variations in the condition index for cows and bulls are illustrated in Fig. 1. Since the linear dimensions of bulls and cows were different it may not be possible to compare absolute values of the condition index between the sexes. However comparison on a relative basis is reasonable.

In agreement with observed weight changes (Chapter V, Fig. 2 and 3), body condition began a steep decline in late February which continued until mid April, leveling off at that time. After the beginning of May, corresponding to the time of initial availability of high quality spring forage, body condition began to improve. The spring and summer (May 2 to August 20) increase in the condition index for bulls ($.22 \pm .01$) was significantly greater ($P<.01$) than for cows ($.10 \pm .03$) as determined by a Students t-test.

Figure 1. Seasonal changes in the mean condition index (ratio of chest girth : hind foot length) for three cow and two bull elk.


CONDITION INDEX
2.70
2.60
2.50
2.40
2.30
S O N D J F M A M J J A S O N D
MONTH
COWS
BULLS

Relationship Between Body Weight and Chest Girth

The relationship between body weight and chest girth was investigated using linear regression analysis. Results are summarized in Table 1.

Although the overall relationship between chest girth and body weight was highly significant ($P<.001$) it was thought that an improvement in statistical reliability could be achieved by considering the influence of pelage type. Consequently the data were separated according to whether the wapiti were in summer or winter coat. During the period May 15 to the end of August the wapiti were considered to be in summer pelage. In all other cases (October 1 to the beginning of May) they were in winter coat. The regression equations resulting from this treatment are presented in Table 1. A t-test revealed that regression coefficients differed significantly ($t = 2.019$, $df = 191$, $P<.05$) for winter and summer pelage types.

Table 1. Linear regression analysis of the relationship between body weight in kilograms (Y) and chest girth measured in centimetres (X) for elk having different pelage types. Weights of cows were corrected for gravid uterus weight.

Pelage Type	Sample Size	Regression equation	r^2	F ratio	Level of Significance	Weight Range (kg)
All cases	195	Y = 3.128X - 244.800	.88	1415.33	P<.001	34.0 to 301.4
Summer	71	Y = 3.520X - 289.010	.90	621.00	P<.001	34.0 to 291.8
Winter	124	Y = 3.101X - 246.811	.92	1403.00	P<.001	50.0 to 301.4

Appendix 3

Body Weight Records

Table 1. Description of experimental animals.

Animal No.	Sex	Year Born	Comments
1129	F	1976	gave birth June 25, 1980
1131	F	1976	gave birth June 15, 1980
1132	F	1976	gave birth June 20, 1980
1134	M	1976	subordinate bull
1136	M	1976	dominant bull
1246	F	1977	
1247	F	1977	
1248	M	1977	
1249	F	1977	born late, July 11, 1977
1301	M	1978	born June 25; raised by dam

Table 2. Original Weight records (Kg).

Date	1129	1131	1132	1134	1136	1246	1247	1248	1249	1301
Aug 31/77	189.0	198.0	197.0	210.0	232.0	58.0	44.5	55.5	34.0	
Oct 06	189.6	212.3	199.6	222.3	236.4	68.2	64.1	79.6	50.0	
Nov 06	198.2	213.6	204.5	222.7	238.6	89.6	77.3	92.7	60.9	
Nov 20	195.9	220.9	207.7	225.5	242.7	94.1	84.1	100.0	65.5	
Dec 03	195.5	221.8	212.3	223.1	241.5	97.7	88.5	101.8	68.6	
Dec 21	200.5	222.7	216.8	220.0	247.7	100.0	90.9	105.0	70.5	
Jan 08/78	198.6	220.5	203.6	220.5	247.7	98.2	91.8	104.6	65.5	
Feb 01	192.7	219.1	200.5	214.6	237.3	97.7	92.3	102.3	65.5	
Feb 20	193.6	215.9	198.2	209.1	230.9	98.6	93.6	103.6	66.4	
Mar 09	183.6	205.0	-	204.5	218.2	97.3	90.5	100.5	61.8	
Mar 30	174.0	184.0	179.0	201.8	216.4	90.9	83.6	95.9	62.7	
Apr 13	-	-	-	201.8	212.3	89.1	85.0	96.4	62.3	
May 02	183.6	189.5	180.9	190.5	202.7	89.1	85.0	97.3	62.7	
May 15	192.7	205.0	190.0	196.8	204.1	95.0	95.5	108.2	73.2	
May 29	208.6	222.7	205.9	216.8	222.7	111.8	111.8	129.1	89.1	
June 13	222.7	-	222.3	231.8	235.9	122.7	127.3	145.5	104.5	
June 25	193.6	204.5	202.7	233.2	238.2	126.4	129.5	152.7	111.8	18.2
July 09	205.0	215.5	216.4	250.0	255.0	144.5	145.5	169.5	126.4	36.4
July 23	216.4	223.6	220.0	259.1	263.6	152.7	155.5	177.3	138.4	-
Aug 06	221.4	231.8	220.5	279.1	280.9	161.4	163.6	193.2	148.6	63.2
Aug 20	226.4	234.1	226.4	290.0	291.8	176.8	178.2	208.6	162.7	78.6
Oct 03	229.1	237.7	235.0	282.7	275.0	198.2	191.8	233.2	177.3	116.8
Dec 17	226.8	238.6	229.1	301.4	294.1	200.0	192.3	228.6	180.9	-
Jan 31/79	218.2	220.5	220.5	281.8	279.1	190.9	186.4	218.2	10.5	134.1

Appendix 4

Crude Protein Content (%) of Wapiti Feces

Feces crude protein content (%) from wapiti.

Day	Year	Sample Size	Mean	Standard Error
10/06	1977	6	15.35	0.43
10/17		8	14.38	0.58
10/24		5	13.60	0.59
11/12		3	13.20	0.35
11/21		5	12.68	0.55
11/29		3	12.90	0.81
12/20		8	11.09	0.24
01/06	1978	6	10.55	0.32
01/22		4	9.75	0.13
02/02		6	9.10	0.19
02/22		6	8.57	0.10
03/07		5	8.48	0.18
03/29		8	10.68	0.14
04/25		6	11.92	0.45

05/10	6	18.92	0.72
05/17	8	20.30	1.14
05/24	10	21.77	0.44
06/06	3	20.83	0.58
06/21	4	21.93	0.23
07/07	12	21.00	0.45
07/13	7	20.34	0.37
07/25	6	20.19	0.89
08/09	1	19.80	-
08/30	10	18.10	0.34
09/30	8	15.78	0.32

Appendix 5

Habitat occupancy by season, time of day and by predominant herd activity.

SEASON: Fall

TIME OF DAY: Early Morning

Activity	Habitat Types						
	Wetland Pond	Sedge Meadow	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	8	6	3	0	5
Browse	0	0	0	0	0	0	0
Drink	0	0	0	0	0	0	0
Bed	0	0	10	6	0	0	3

SEASON: Fall

TIME OF DAY: Morning

Activity	Habitat Type						
	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest	
Stand	0	2	1	0	0	0	1
Walk	0	0	0	2	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	10	48	15	6	2	32
Browse	0	6	10	0	0	0	20
Drink	0	4	0	0	0	0	0
Bed	0	2	15	0	0	6	18

Habitat Types

Activity	Pond	Wetland Sedge Meadow	Upland Meadow	Lowland Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	2	0	0	0	0	1
Run	0	0	0	0	0	0	0
Graze	0	0	28	4	0	23	15
Browse	0	3	1	0	0	1	3
Drink	0	0	0	0	0	1	0
Bed	0	0	0	6	0	33	25

SEASON: Fall

TIME OF DAY: Evening

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	1	0	2	7	0	7	8
Browse	0	1	0	0	0	0	1
Drink	0	0	0	0	0	0	0
Bed	6	0	0	0	0	5	1

SEASON: Fall

TIME OF DAY: Night

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	64	0	0	0	2
Browse	0	0	0	0	0	0
Drink	0	0	0	0	0	0
Bed	0	78	0	0	0	0

SEASON: Early Winter

TIME OF DAY: Early Morning

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	4	0	0	2	5
Browse	0	0	0	0	0	0	10
Drink	0	0	0	0	0	0	0
Bed	0	0	0	0	0	0	0

SEASON: Early Winter

TIME OF DAY: Morning

Habitat Types

Activity	Wetland Pond	Upland Sedge	Lowland Meadow	Treated Meadow	Willow Posts	Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	1	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	2	11	0	0	0	4
Browse	0	0	0	0	0	0	20
Drink	0	0	0	0	0	0	0
Bed	0	0	5	0	0	0	36

SEASON: Early Winter

TIME OF DAY: Afternoon

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	2	12	2	0	4
Browse	0	0	0	0	0	8
Drink	0	0	0	0	0	0
Bed	0	0	18	0	0	2

SEASON: Early Winter

TIME OF DAY: Evening

Activity	Habitat Types						
	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	1	0	0	0	0
Walk	0	0	1	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	4	0	0	0	0
Browse	0	0	0	1	0	0	3
Drink	0	0	0	0	0	0	0
Bed	0	0	7	0	0	0	0

SEASON: Early Winter

TIME OF DAY: Night

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	4	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	4	0	22	27	0	0	11
Browse	0	0	3	0	0	0	2
Drink	0	0	0	0	0	0	0
Bed	0	0	2	32	0	0	37

SEASON: Mid Winter

TIME OF DAY: Early Morning

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	0	0	0	0	1
Browse	0	0	3	1	0	0	4
Drink	0	0	0	0	0	0	0
Bed	0	0	1	2	0	0	0

SEASON: Mid Winter

TIME OF DAY: Morning

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	11	0	0	0	3
Browse	0	4	3	0	0	2	21
Drink	0	0	0	0	0	0	0
Bed	0	0	0	0	0	0	12

SEASON: Mid Winter

TIME OF DAY: Afternoon

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	4	0	0	0	0
Browse	0	1	0	0	5	7
Drink	0	0	0	0	0	0
Bed	0	35	0	0	14	12

SEASON: Mid Winter

TIME OF DAY: Evening

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	8	1	0	0	0
Browse	0	0	1	0	0	4	23
Drink	0	0	0	0	0	0	0
Bed	0	0	3	0	0	0	0

SEASON: Mid Winter

TIME OF DAY: Night

Activity	Habitat Types						
	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest	
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	26	0	0	0	1
Browse	0	0	0	1	0	9	18
Drink	0	0	0	0	0	0	0
Bed	0	0	51	0	0	0	2

SEASON: Late Winter

TIME OF DAY: Early Morning

Activity	Habitat Types						
	Pond	Wetland Sedge Meadow	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	2	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	4	0	0	0	0
Browse	0	0	4	0	0	0	3
Drink	0	0	0	0	0	0	0
Bed	0	0	8	0	0	0	2

SEASON: Late Winter

TIME OF DAY: Morning

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	5	1	0	0	0	0
Walk	0	0	1	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	3	1	31	0	1	0	1
Browse	2	0	1	0	0	0	29
Drink	0	0	0	0	0	0	0
Bed	0	0	13	0	0	0	24

SEASON: Late Winter

TIME OF DAY: Afternoon

Activity	Habitat Types						
	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	2	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	1	0	49	2	0	0	0
Browse	0	0	0	0	0	0	2
Drink	0	0	0	0	0	0	0
Bed	2	0	47	0	0	0	10

SEASON: Late Winter

TIME OF DAY: Evening

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	31	0	0	0	0
Browse	0	0	0	0	0	2
Drink	0	0	0	0	0	0
Bed	0	14	0	0	0	0

SEASON: Late Winter

TIME OF DAY: Night

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	0	24	0	0	0
Browse	0	0	0	0	6	0
Drink	0	0	0	0	0	0
Bed	0	0	20	0	3	0

SEASON: Early Spring

TIME OF DAY: Early Morning

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	9	0	5	0	2
Browse	0	0	0	0	0	0	0
Drink	0	0	0	0	0	0	0
Bed	0	0	6	0	0	0	0

SEASON: Early Spring

TIME OF DAY: Morning

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	1	0	0	0
Run	0	0	0	0	0	0
Graze	0	11	39	7	0	3
Browse	0	0	0	0	0	1
Drink	0	0	0	0	0	0
Bed	0	0	35	0	0	11

SEASON: Early Spring

TIME OF DAY: Afternoon

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	1	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	12	20	0	0	0	5
Browse	0	0	1	0	0	0	3
Drink	0	0	0	0	0	0	0
Bed	0	14	28	15	0	3	14

SEASON: Early Spring

TIME OF DAY: Evening

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	27	3	0	0	7
Browse	0	0	0	0	0	0	6
Drink	0	0	0	0	0	0	0
Bed	0	0	3	1	0	2	2

SEASON: Early Spring

TIME OF DAY: Night

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	1	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	12	0	0	0	0
Browse	0	0	0	0	0	0	0
Drink	0	0	0	0	0	0	0
Bed	0	0	1	0	0	0	0

SEASON: Spring

TIME OF DAY: Early Morning

Activity	Habitat Types						
	Wetland Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Willow Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	1	2	0	0	6
Browse	0	0	0	0	0	0	0
Drink	0	0	0	0	0	0	0
Bed	0	0	2	0	0	0	1

SEASON: Spring

TIME OF DAY: Morning

Activity	Habitat Types						
	Pond	Wetland Sedge Meadow	Upland Meadow	Lowland Meadow	Treated Willow Posts	Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	5	19	3	4	9	32
Browse	0	2	0	0	0	2	1
Drink	0	0	0	0	0	0	0
Bed	0	10	39	0	7	6	10

SEASON: Spring

TIME OF DAY: Afternoon

Activity	Habitat Types						
	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest	
Stand	0	0	1	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	2	3	39	10	1	3	25
Browse	0	5	1	0	0	0	3
Drink	0	0	0	0	0	0	1
Bed	0	4	67	33	20	9	46

SEASON: Spring

TIME OF DAY: Evening

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	1	0	0	0
Walk	0	0	1	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	2	1	41	8	2	5	29
Browse	0	0	0	0	0	1	0
Drink	0	0	0	0	0	0	0
Bed	0	0	26	1	5	3	8

SEASON: Spring

TIME OF DAY: Night

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	0	17	2	0	9
Browse	0	0	0	0	0	2
Drink	0	0	0	0	0	0
Bed	0	0	64	0	0	24

SEASON: Summer

TIME OF DAY: Early Morning

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	0
Run	0	0	0	0	0	0
Graze	0	0	15	5	0	2	6
Browse	0	0	0	0	0	0	0
Drink	0	0	0	0	0	0	0
Bed	0	0	3	0	0	1	13

SEASON: Summer

TIME OF DAY: Morning

Activity	Habitat Types						
	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest	
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	1	26	5	0	1	11
Browse	0	0	0	3	0	0	4
Drink	0	0	0	0	0	0	0
Bed	0	3	43	24	87	0	13

SEASON: Summer

TIME OF DAY: Afternoon

Activity	Habitat Types						
	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest	
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	1	56	7	4	9	9
Browse	0	0	0	0	0	0	0
Drink	0	0	0	0	0	0	0
Bed	0	29	38	26	232	1	26

SEASON: Summer

TIME OF DAY: Evening

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	1	0	0	0	0
Walk	0	0	0	0	0	0	1
Run	0	0	0	1	0	0	0
Graze	0	1	25	4	1	5	12
Browse	0	0	1	0	0	1	7
Drink	0	0	0	0	0	0	0
Bed	2	0	18	0	6	2	27

SEASON: Summer

TIME OF DAY: Night

Habitat Types

Activity	Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	3	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	1	14	2	0	3	11
Browse	0	2	0	0	0	1	2
Drink	0	0	0	0	0	0	0
Bed	0	0	29	0	0	0	0

SEASON: Late Summer

TIME OF DAY: Early Morning

Activity	Habitat Types						
	Wetland Pond	Wetland Sedge	Upland Meadow	Lowland Meadow	Treated Willow Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	1	0	0	0	2
Browse	0	0	1	0	0	1	5
Drink	0	0	0	0	0	0	1
Bed	0	0	12	0	0	0	4

SEASON: Late Summer

TIME OF DAY: Morning

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	2	0	0	0	0
Walk	0	0	0	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	1	0	4	2	0	0	1
Browse	1	0	0	3	0	1	7
Drink	0	0	0	0	0	0	0
Bed	0	0	7	0	0	0	12

SEASON: Late Summer

TIME OF DAY: Afternoon

Activity	Habitat Types						
	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest	
Stand	0	0	5	0	0	0	3
Walk	0	0	0	0	0	0	2
Run	0	0	0	0	0	0	0
Graze	0	0	0	0	0	0	2
Browse	0	0	0	0	0	0	3
Drink	0	0	1	0	0	0	0
Bed	0	0	5	0	0	0	9

SEASON: Late Summer

TIME OF DAY: Evening

Activity	Habitat Types						
	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest	
Stand	0	0	2	0	0	0	6
Walk	0	0	1	0	0	0	0
Run	0	0	0	0	0	0	0
Graze	0	0	5	1	0	1	8
Browse	0	0	0	2	0	0	6
Drink	0	0	0	0	0	0	0
Bed	0	0	9	0	0	0	17

SEASON: Late Summer

TIME OF DAY: Night

Habitat Types

Activity	Wetland Pond	Upland Sedge Meadow	Lowland Meadow	Treated Posts	Willow Fringe	Forest
Stand	0	0	0	0	0	0
Walk	0	0	0	0	0	2
Run	0	0	0	0	0	0
Graze	0	0	12	0	0	2
Browse	0	0	1	9	0	5
Drink	0	0	0	0	0	0
Bed	0	0	25	0	0	2

Appendix 6

Daily Activities of Wapiti in Each Season, Based on Observation Records of Individual Animals

SEASON: Fall

Activity	Time of Day: Early Morning	Morning	Afternoon	Evening	Night
Stand	3	40	10	12	0
Walk	0	26	18	1	0
Run	0	0	0	0	0
Graze	168	849	515	191	610
Browse	11	312	127	24	0
Drink	0	26	11	0	0
Bed	144	381	581	117	686
Other	6	73	1	0	0

SEASON: Early Winter

Activity	Time of Day				
	Early Morning	Morning	Afternoon	Evening	Night
Stand	3	14	0	9	27
Walk	0	2	0	5	0
Run	0	0	0	0	0
Graze	98	128	158	43	486
Browse	82	158	91	37	143
Drink	0	0	0	0	0
Bed	2	347	208	58	639
Other	0	2	0	0	0

SEASON: Mid Winter

	Time of Day				
Activity	Early Morning	Morning	Afternoon	Evening	Night
Stand	0	0	3	4	0
Walk	0	0	0	0	0
Run	0	0	0	0	0
Graze	20	112	66	89	221
Browse	40	226	158	212	251
Drink	0	0	0	0	0
Bed	27	130	487	43	489
Other	0	0	0	0	0

SEASON: Late Winter

Time of Day

Activity	Early Morning	Morning	Afternoon	Evening	Night
Stand	10	51	8	3	1
Walk	0	21	3	1	0
Run	0	0	0	0	0
Graze	11	260	359	255	162
Browse	66	276	90	21	67
Drink	0	0	0	0	0
Bed	97	280	559	118	228
Other	3	11	2	0	3

SEASON: Early Spring

	Time of Day				
Activity	Early Morning	Morning	Afternoon	Evening	Night
Stand	0	3	2	0	0
Walk	0	15	9	0	9
Run	0	0	0	0	0
Graze	104	508	341	336	69
Browse	8	27	59	50	0
Drink	0	0	0	0	0
Bed	49	420	592	97	48
Other	0	4	11	0	0

SEASON: Spring

Activity	Time of Day: Early Morning	Morning	Afternoon	Evening	Night
Stand	0	0	9	16	0
Walk	2	0	0	6	0
Run	0	0	4	4	0
Graze	36	385	726	604	177
Browse	3	32	39	26	10
Drink	0	0	7	2	0
Bed	9	352	1323	303	539
Other	0	0	0	0	0

SEASON: Summer

Activity	Time of Day				
	Early Morning	Morning	Afternoon	Evening	Night
Stand	13	19	9	13	16
Walk	7	10	1	4	10
Run	0	3	0	5	1
Graze	128	252	777	314	161
Browse	3	50	10	48	22
Drink	0	0	2	2	0
Bed	70	1104	2428	263	163
Other	0	0	0	0	0

SEASON: Late Summer

	Time of Day				
Activity	Early Morning	Morning	Afternoon	Evening	Night
Stand	0	22	43	31	0
Walk	1	11	15	8	8
Run	0	0	0	0	0
Graze	20	32	24	106	65
Browse	26	24	15	47	55
Drink	3	0	4	0	0
Bed	23	105	71	126	110
Other	3	0	0	4	0